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CORRIGENDA

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p. 13, l. 10: *for inhibitions read inhibition*
p. 15, l. 6: *for darkness read darkness**
p. 16, l. 8: *for Lamium. read Lamium*
p. 18, l. 1: *for Short white read stimulating*
p. 18, l. 12: *for Parier read Parker*
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termination of
Atman-Zahavi

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in the cucum-
d D. Atsmon

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EFFECTS OF SHORT AND CONTINUOUS ILLUMINATIONS ON THE GERMINATION OF *AMARANTHUS RETROFLEXUS* SEEDS*

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ABSTRACT

The effects of light on the germination of *Amaranthus retroflexus* seeds were investigated. It was found that:

1. A certain percentage of the seeds germinated in darkness. This germination could be inhibited by white light when applied continuously from sowing, F. R. being the active part. The majority of the seeds needed a light stimulus in order to germinate. A few seconds of white or red illumination was enough to cause full germination. Maximum sensitivity towards this stimulating illumination was reached only two or more days after sowing.

2. The well known reversible R-F.R. reaction was operative in these seeds but it was found that when F. R. illumination was applied for prolonged durations (hours instead of seconds) subsequent red illumination failed to promote germination. This was termed: The prolonged F. R. effect. The responsiveness of the seeds to stimulating red illumination could be recovered after a certain dark period.

3. In the reversible R-F.R. reaction the inhibition by F.R. was found to be maximal when F. R. was applied not immediately after the red, but after an interval of 2-16 minutes. Low temperature during this interval further delayed the time of maximal effectiveness of F. R. This fact suggested that F. R. reversed a temperature-sensitive dark-reaction that followed the red reaction.

4. The possible relationships between the different inhibiting effects of F. R. have been discussed and some of the implications of the prolonged F. R. effect on seed germination, on internode elongation and on other formative and photoperiodic phenomena in plants have been pointed out.

INTRODUCTION

The effect of light on germination differs in many cases according to whether the germinating seeds are kept under continuous light or whether they are irradiated for a short time. For lettuce seeds subjected to short periods of irradiation, the germination percentage is directly proportional to light intensity; but it is inversely proportional to light intensity under continuous illumination (Evenari 1952). In *Eschscholzia californica* and *Amaranthus fimbriatus* (Soriano 1953) and in *Nigella* (Isikawa 1957) germination was inhibited by continuous illumination, but a single exposure some time after sowing greatly enhanced germination. Similarly, Isikawa *et al.* (1954, 1955) found that in many seeds repeated daily illuminations or a single

* This paper is based on a Ph. D thesis submitted to the Senate of The Hebrew University of Jerusalem.

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short illumination promoted germination more than continuous illumination. This was considered to be a photoperiodic effect on germination. A similar response was reported for *Amaranthus blitoides* (Kadman-Zahavi 1955).

This difference between the effects of short and continuous illumination forms the subject of the present study.

MATERIALS AND METHODS

After preliminary screening, *Amaranthus retroflexus* (*A.r.*) was chosen as the most suitable experimental material.

The seeds were collected in Jerusalem on August 3rd, 1954. With one exception, all the experiments reported here were carried out with these seeds. The seeds were stored in dark glass bottles and kept in a dark place, at room temperature. Germination was carried out in small petri-dishes on a double layer of filter paper wetted with distilled water. One hundred seeds were usually placed in each dish and three dishes were used for each treatment. Each experiment was repeated several times on different dates. *Variability* is given as the actual maximum deviation from the mean (+ or -). Seedlings were counted in the dark room before each treatment.

The experiments reported here were conducted, when not otherwise stated, at 37°C, in a water-jacketed thermostat topped by a glass tray in which a constant current of water was circulated. The lamps were placed outside the thermostat in such a way as to provide a wide space of uniform illumination. It was possible to place twenty dishes under equal conditions of illumination and temperature. Light intensity was regulated either by changing the distance of the lamps from the thermostat, or by placing the seeds at different levels inside the thermostat. For germination in darkness the petri-dishes were placed inside tin boxes. These were opened only in the dark room. The temperature of the dark room was maintained at 26°. Light for work was filtered through a blue Corning-glass filter No. 430. This light was found to be inactive with regard to *A.r.* seed germination (Kadman-Zahavi 1959).

ILLUMINATIONS AND FILTERS

When not otherwise stated, incandescent light was used. Light measurements were carried out with an Everet-Edumbe light meter. For light passed through coloured filters intensity is given as that of the white source at the level of the seeds. No attempt was made to determine light energy in the different wave lengths.

For short illuminations, white incandescent light was usually used for stimulatory radiation. When red light was employed, it was filtered out of the same incandescent source by means of Red Corning Glass Filter No. 245. Transmission curve for this filter was available only up to 700 m μ . F.R. was secured with a Kodak Wratten Gelatine Filter No. 88a, using the same source.

For continuous illuminations, the dishes were wrapped in blue or red cellophane. A Cu(NO₃)₂ solution was used to absorb the F.R. (Evenari and Neumann 1953a). This solution took out most of the F.R. but a greater part of the red as well. The

transmission of the filters was measured with a Beckman photometer. Both the red and the blue filters transmitted most of the F.R. beyond 725 m μ . The blue filter transmitted some red light below 675 m μ . This red light could be removed by a combination of two or more sheets of blue cellophane (Figure 1). The red filter did not transmit any blue light; thus a combination of blue and red filters transmitted only F.R.

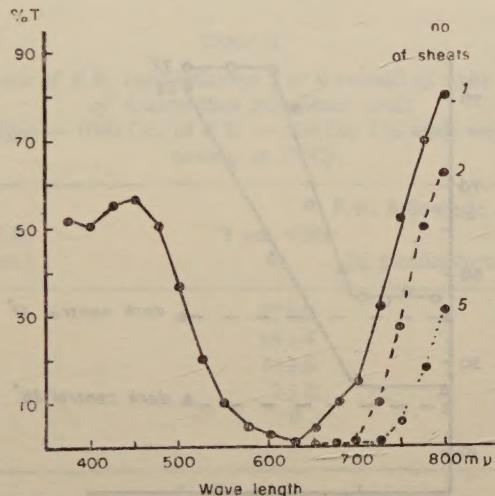


Figure 1
Transmission curves of 1, 2 or 5 sheets of blue cellophane.

EXPERIMENTAL RESULTS

A. retroflexus seeds germinated to a certain extent in darkness; the rate and final percentage of this germination differed with temperature (Table I). At all temperatures dark germination was completed within a short and well defined time from sowing. After that there was no further germination in darkness as long as conditions were not changed.

TABLE I

Germination of Amaranthus retroflexus seeds in darkness at different temperatures

Temperature (°C)	% germination	Time from sowing when germination was complete
20	30±3	5 days
26	31±4	50 hrs
30	36±6	40 hrs
37	44±3	30 hrs
40	0	—

Stimulating illuminations

A short red or white illumination given at different intervals after sowing greatly stimulated germination. The response of the seeds to a short illumination increased up to the third or fourth day, depending on temperature (Figure 2). This response did not diminish when the seeds had been imbibed for two months in the dark at 37°C.

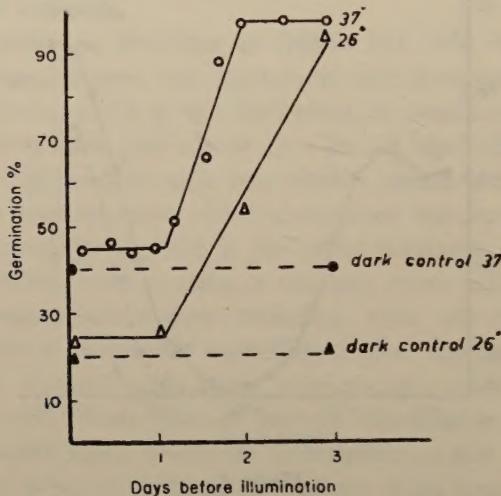


Figure 2

Germination of *Amaranthus retroflexus* seeds in response to short white illuminations (60×10^3 f. c. sec), given at different intervals after sowing in darkness at 37°C or 26°C.

At the time of highest sensitivity the light quantity needed for full stimulation was small, illuminations of 3 sec with 1000 f.c. of white light (3×10^3 f.c. sec) being already within the range of light saturation (Figure 7a). The time needed for complete germination of seeds which had received a short light stimulus was 20 hours after illumination at 37°C, and 40 hours at 26°C.

As the sensitivity of the seeds to light developed fully only two or three days from sowing, and as by that time dark germination had already ceased, it was possible to differentiate the seeds into two physiological groups. One group comprised the seeds which, given the right temperature, started to germinate as soon as they were imbibed. Henceforth, the germination of these seeds will be called *Dark-germination* or *Initial germination* (the latter term will be used whenever the seeds were germinated in light, in order to designate that part of the seeds which did not need light for germination). The other group comprised the seeds which needed a light stimulus

in order to germinate. The effects of the various factors on germination were evaluated separately for each group.

The reversible red-F.R. reaction

A short F.R. illumination reversed the effect of previously applied red (or white) illumination (Table II). This has been shown by Borthwick *et al.* (1952) to be the case for other seeds.

TABLE II

Effects of different amounts of F.R. light following 3 or 6 seconds of white light, on the germination of Amaranthus retroflexus seeds

Intensity of the white light — 1000 f.c., of F.R. — 300 f.c. The seeds were irradiated 48 hrs after sowing at 37°C

Duration of F.R. illumination (sec.)	F.R. following:	
	3 sec white	6 sec white
0	97±2	94±4
60	86±4	77±6
120	14±6	39±9
180	2±2	21±1
300	0	0

* % of illuminated seeds.

Whenever red illumination was given after such a *short F.R.* illumination, full stimulation was again evident.

Interval between red and F.R. illuminations

Experiments were undertaken to investigate whether F.R. directly reverses the photochemical reaction initiated by the red light (Evenari *et al.* 1953); or whether the photochemical reaction is followed by a dark reaction and this reaction is reversed by F.R. (Liverman and Bonner 1953). It was assumed that in the latter case F.R. would be effective only by the time the dark reaction was already underway or completed. It was also assumed that if the reaction was a fast one illumination periods should be very short in order to detect it. Experiments were accordingly carried out in which the length of the time interval between the first short white illumination and the subsequent F.R. illumination was varied.

Since, if a dark reaction exists, it might be expected to be temperature-sensitive, the effect of temperature during this time interval was also investigated by placing one series of dishes for five minutes on crushed ice. It had been first ascertained that this treatment did not in itself affect the response of the seeds to light (Kadman-Zahavi 1959). The results of a typical experiment are given in Figure 3.

It will be seen that F.R. did not reach its maximal effectiveness until two minutes after the white illumination. Furthermore, the temperature prevailing during the interval had a very marked influence: the first reading indicated that the degree of inhibition produced by the F.R. was four times as great at room temperature as it was at 0°C (cf. Figure 3). This discrepancy was gradually reduced with increasing length of the interval and became negligible after four minutes, which suggests that the effect of the low temperature is to delay the time of maximal effectiveness of F.R.

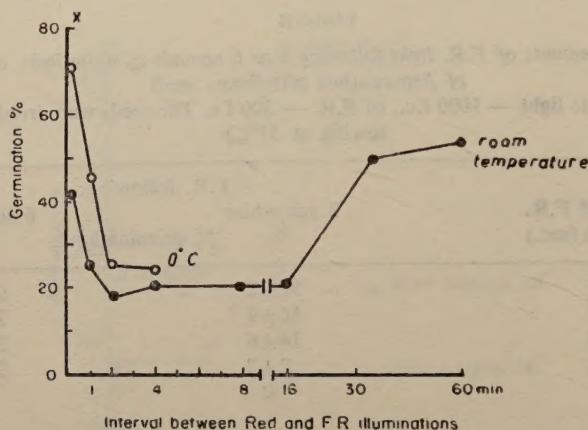


Figure 3

Effect of temperature and of time interval between the application of red and F.R. illuminations on the effectiveness of F.R.

Two days after sowing the seeds received a short white illumination (2 sec \times 1000 f. c.) and subsequently, after various time intervals, a short F.R. illumination (30 sec \times 1000 f. c.). One lot of seeds was kept at room temperature throughout. A second lot was placed on crushed ice for 5 minutes, the white illumination being applied at least 1 minute after the seeds were placed on the ice. The seeds were removed from the ice immediately after the F.R. illumination, and were returned to darkness at 37°C. Germination was estimated 2 days later.

A time interval is thus required after the initial illumination, before the F.R. achieves maximum effectiveness; low temperature during this interval retards this development. These facts provide strong evidence for the involvement of a temperature-sensitive dark reaction in the reversible R:F.R. effect. A delayed effect of F.R. has also been reported by Klein *et al.* (1957) who studied the responses of the hypocotyl hook of beans.

The fact that four minutes after the white illumination the effect of temperature is no longer evident may explain why Borthwick *et al.* (1954) using a different method of investigation could not find any temperature effect on this reaction.

Germination under continuous illumination

Figures 4 and 5d show the germination of *A. retroflexus* seeds at 37°C under continuous illuminations with different intensities of white incandescent light.

It may be seen that under continuous illuminations there are two germination periods: A number of seeds germinate during the first day. There is very little additional germination between the first and second day and then a second period of high germination follows. By the fifth day germination in continuous illumination is almost complete. The first period probably coincides with the "initial germination", the second, with the time of high sensitivity to short illumination. In the first period light inhibited germination, this inhibition being directly proportional to the logarithm of light intensity (Figure 4, the curves for the first and second day). In the second period (the third and subsequent days in Figure 4) the curves rise to a peak at about 150 f.c. This suggests that during the second period white light had at least two antagonistic effects—one stimulating, the other inhibiting germination.

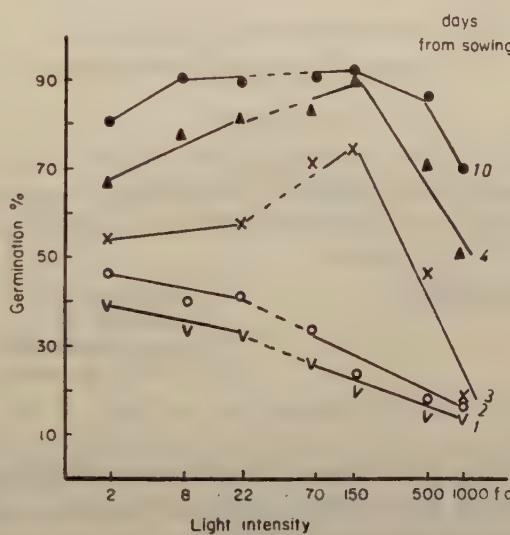


Figure 4

Germination of *Amaranthus retroflexus* seeds under different intensities of white incandescent light. (Each line represents germination up to a certain day after sowing. The day is indicated on the right hand side of the line. On the abscissa: Light intensity on a logarithmic scale).

The effects of continuous illumination with light of different colours was studied using blue or red cellophane filters with or without a F.R. absorbing solution (Figure 5).

The initial germination was inhibited to the same extent by all light combinations. In F.R. light or in blue plus F.R. there was no further germination after completion of the initial germination, while under the red filter as well as in white light, i.e. in lots that received the red part of the spectrum, germination was stimulated above the initial germination.

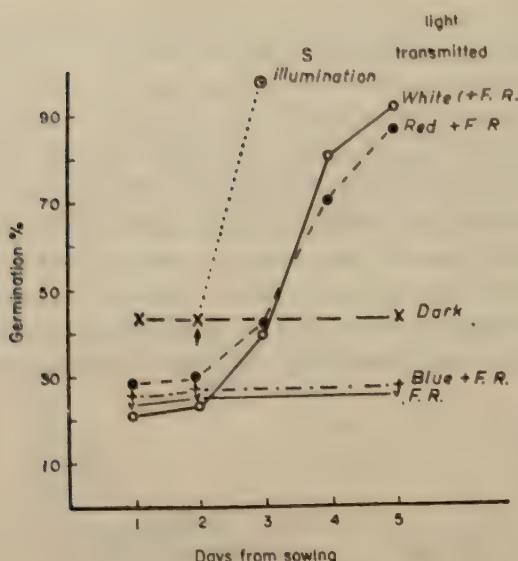


Figure 5

Germination of *Amaranthus retroflexus* seeds in continuous light transmitted through different filters at 37°C (Lettering indicates light transmitted).

The filters:

✓ Red + blue cellophane	○ White light
+ Blue	✗ Darkness
● Red	⊖ Short illumination
"	(3×10^3 f.c. sec white, 48 hrs from sowing).

No difference could be found between germination in light that passed through the red filter and that in white light. Likewise, there was no difference between germination under the blue filter and that under the blue plus red filter combination. This suggested that blue light had no effect on the germination of *A. r.* seeds. This was further confirmed when F.R. was filtered out of the light that passed through the blue filter (Figure 6).

Filtering out the F.R. removed almost all the light-induced inhibition.

It may, therefore, be concluded that both in the case of continuous and short illumination, red light stimulated and F.R. light inhibited germination. This, however, did not answer the question why continuous illumination with white light inhibited germination as compared with short illumination with the same light.

Darkness after continuous illumination

The question had been raised whether transfer to darkness would restore the ability of the dark-germinating seeds to germinate in darkness (Jones and Bailey 1956). It was found that on transfer to darkness from white or red light a number of seeds

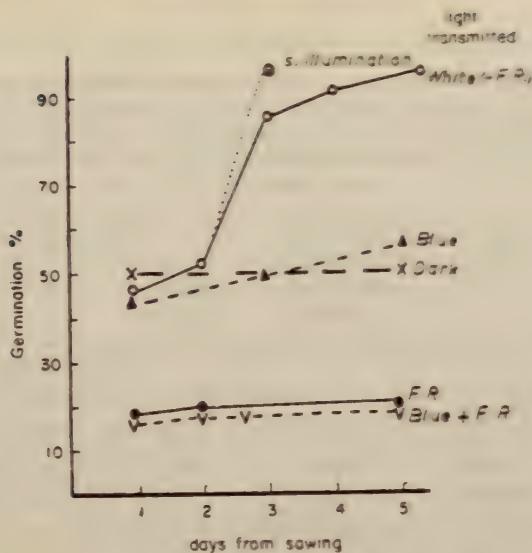


Figure 6

Germination of *Amaranthus retroflexus* seeds in continuous light with or without F. R. at 37°C (Lettering indicates light transmitted).

The filters:

● Red + blue cellophane	○ 1 cm F. R. absorbing solution
▼ Blue	✗ Darkness
▲ Blue cellophane + 1 cm	⊖ Short illumination
F. R. absorbing solution	(3×10^3 f.c. sec white, 48 hrs from sowing).

germinated, while not a single seed germinated in dishes that had been first kept in F.R. light (or F. R. + blue). It was further determined that germination in darkness was complete by about 30 hours after transfer. The number of germinating seeds corresponded closely with that of control dishes kept in light during the same time (Table III). The amount of germination in darkness after a period in continuous illumination thus depended on the colour of the light, on light intensity, and on the time of transfer.

Red after continuous F.R.

It has already been shown (Table II) that the stimulation of a short red illumination could be reversed by a short F.R. illumination, and it has been stated that this inhibition could be completely offset by a subsequent red illumination. It was considered important to ascertain whether red illumination would also cancel the inhibitory effect of continuous F.R. illumination. The effect of short white illumination on seeds that had been kept for two days in F.R. was therefore compared with that on seeds maintained in darkness for the same period (Figure 7).

It is clearly evident that the inhibitory effect of prolonged F.R. could not be overcome by a subsequent short white illumination. At the end of two days in F.R.,

TABLE III

Germination of Amaranthus retroflexus seeds in darkness after different periods in continuous white light
 (The seeds were kept in continuous white light of different intensities at 37°C. At the end of 2 or 11 days one lot in each group was transferred to darkness, while the other was kept for an additional two days in continuous light. Germination was estimated before the transfer and again after two days).

Date	Light int. (f.c.)	Days in con- tinuous illum- ination before transfer	% germination		
			Before transfer	2 days after transfer	
			in dark	in light	
13.5.56	400	2	17	32	29
6.7.56	400	2	16	30	36
10.12.56	500	11	89	1	0
10.12.56	1000	11	69	7	1

the response of the seeds to a stimulatory irradiation was very weak and even at saturating amounts of light the percentage of germinating seeds did not reach the level of the initial dark germination. This implies that, apart from inhibiting the initial germination, continuous F.R. illumination inhibited the development of responsiveness towards a stimulating irradiation which in dark sown seeds reaches

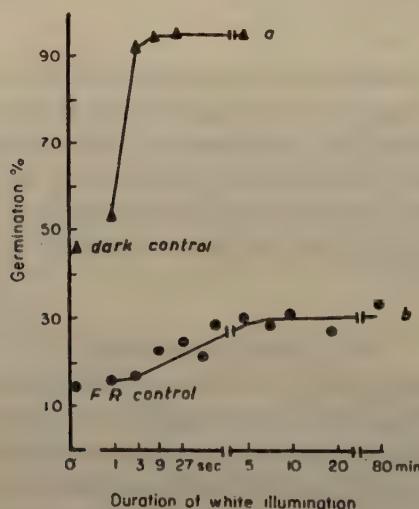


Figure 7

The response of *Amaranthus retroflexus* seeds to short white illumination (1000 f. c.) after 2 days in darkness or continuous F. R.

- Seeds kept in darkness for 2 days before the illumination;
- Seeds kept in F. R. (1000 f. c.) for 2 days before the illumination.

sts peak after two days (cf. Figure 2). Further it was investigated whether prolonged F.R. would bring the seeds into a state of "light-dormancy" (Evenari 1956) or whether the seeds would recover their responsiveness to red after the removal of F.R. A representative experiment set up to solve this problem is summarized in Table IV A. There was no difference between the final germination figures for lots 3 and 4, i.e., the effect of a short white illumination was the same for seeds transferred to darkness after two days in F.R. and seeds maintained throughout in darkness. This demonstrated that a certain period in darkness restores the responsiveness of the seeds to stimulating irradiation.

Additional experiments were designed to ascertain whether F.R. merely prevented the development of sensitivity of the seeds to red light or whether it would also reduce the response when applied at the time of highest sensitivity. These experiments are summarized in Table IV B. It is evident that prolonged F.R. illumination reduced the sensitivity of the seeds to red light even when applied at a time when this sensitivity was high. At the end of the experiment represented in Table IV B (six days from sowing), the seeds of lot 2 received a short white illumination. Within two days 98 per cent of the seeds germinated. Thus the responsiveness of *A. retroflexus* seeds to red illumination could be changed repeatedly by subjecting the seeds alternately to darkness and F.R. light (see Figure 12).

TABLE IV

A. Effect of darkness following continuous F.R. illumination on the response of *A. retroflexus* seeds to a short white illumination

B. Effect of continuous F.R. illumination following darkness on the response of *A. retroflexus* seeds to a short white illumination (37°C).

(Seeds collected in 1956 were used in this experiment)

2 days F.R. 1000 f.c.

2 days darkness

60×10^3 f.c. sec of white light

A.

Lot No.				% germination
1	-----	*	-----	21±1
2	-----	*	-----	43±4
3	-----	*	-----	98±2
4	-----	*	-----	98±4

B.

Lot No.				% germination	a	b	c
1	-----	-----	*	2±2			
2	-----	-----	*	0			
3	-----	-----	*	100±0			

a % of illuminated seeds.

b Initial dark germination was 44±7%.

c A certain number of seeds (about 10%) germinated under the blue cellophane used as a F.R. filter. Filtering out the residual red with an additional sheet of blue cellophane (Figure 1) prevented this germination.

The time course of reduction of sensitivity to red by exposure to continuous F.R. at 37°C is represented in Figure 8. It is apparent that under these conditions the seeds no longer respond to short illumination, after having been exposed to F.R. light for about 30 hours.

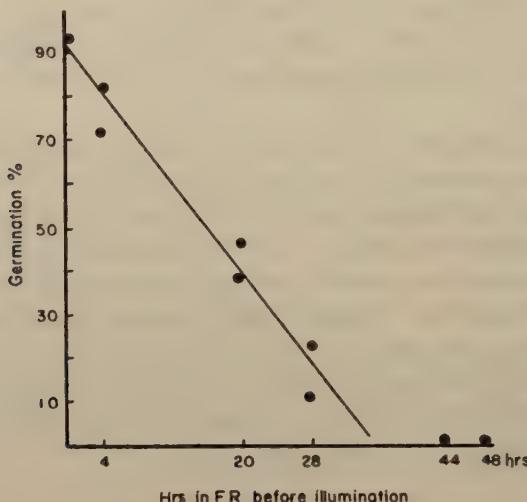


Figure 8

Time course of the reduction of the sensitivity to stimulating illumination by exposure to continuous F. R. light. The seeds were kept for 2 days in darkness and subsequently for different durations in F. R. (1000 f. c.), then illuminated with 3×10^3 f. c. sec of white light and transferred to darkness. Germination was estimated 2 days later. Dark-germinated seedlings were removed before transfer to F. R.
(Seeds collected in 1956 were used for this experiment).

They are, however, capable of recovering their sensitivity to red illumination if kept in darkness. The time course of such recovery at 37°C is presented in Figure 9.

The effect of blue light

Many authors (Flint and McAllister 1935, Meischke 1936, Resähr 1939 and Evenari *et al.* 1957) have reported inhibiting effects caused by the blue zone of the spectrum. As already reported here (cf. Figure 6) the blue light, when free, of any far-red, did not affect the initial germination of *A. r.* seeds. It was shown (Table V) that blue light also had little effect on the response of the seeds to red illumination. The small difference between the dark control and the blue light series may probably be attributed to residual amounts of far-red still passing through the filters. The discrepancy between our results and those of the other authors regarding the effect of blue light may possibly be due to a lowered transmission of the black seed coats of the *A. r.*

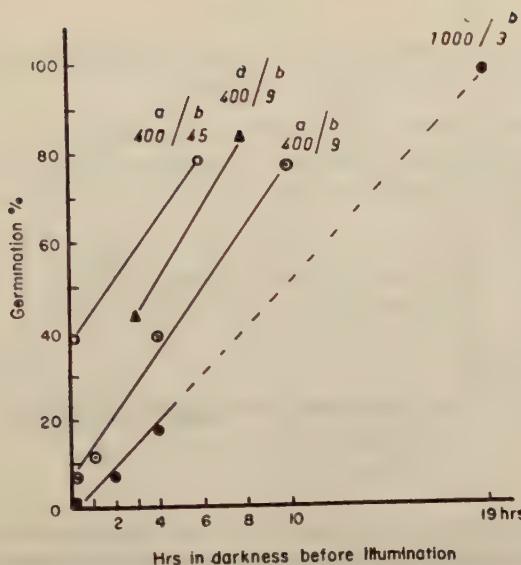


Figure 9

Time course of the recovery of the sensitivity of *Amaranthus retroflexus* seeds to stimulating illuminations. The seeds were kept at 37°C for 2 days in continuous F. R. and subsequently for varying time intervals in darkness, and then illuminated. The seedlings of the initial germination were removed before transfer to darkness. Each line represents a different experiment.

- a. Light intensity of continuous F. R. (400 or 1000 f. c.).
- b. Duration (sec) of short illumination with 1000 f. c. of white light.

to short parts of the spectrum. A similar phenomenon was reported by Meischke (1936) and Evenari (1956) for many other seeds.

The fact that blue light was found to be neutral in the germination of *A. r.* seeds made it possible to use the blue cellophane alone as a F.R. filter. It may be seen from Figure 1 that in addition to most of the F.R. above 725 m μ the blue filter also transmitted some red below 700 m μ . In order to make sure that this residual red light did not contribute to the above mentioned inhibiting effects, the experiments were repeated using two or more sheets of blue cellophane. In this way all wavelengths below 700 m μ were eliminated (cf. Figure 1). It was found that even light that had passed through five sheets of blue cellophane caused significant inhibitions of the initial germination as well as a reduction in the responsiveness of the seeds to red light (Kadman-Zahavi 1959).

Intensity of F.R.

The influence of intensity of F.R. on the initial germination and on the sensitivity of the seeds to red is summarised in Figures 10 and 11.

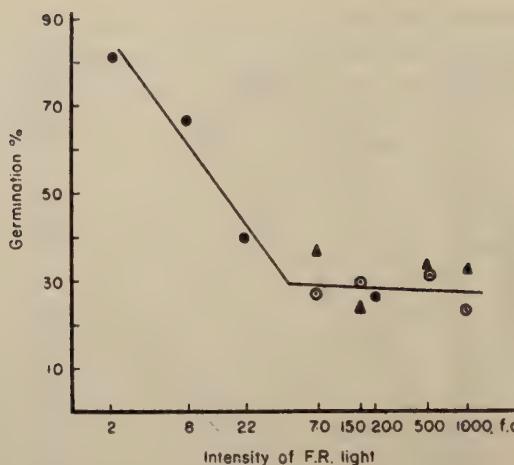


Figure 10

Relationship between intensity of prolonged F.R. illumination and initial germination.
Amaranthus retroflexus seeds were germinated in continuous F.R. at different intensities at 37°C.
 Germination was estimated 2 days after sowing.
 (On the abscissa: Light intensity on a logarithmic scale).

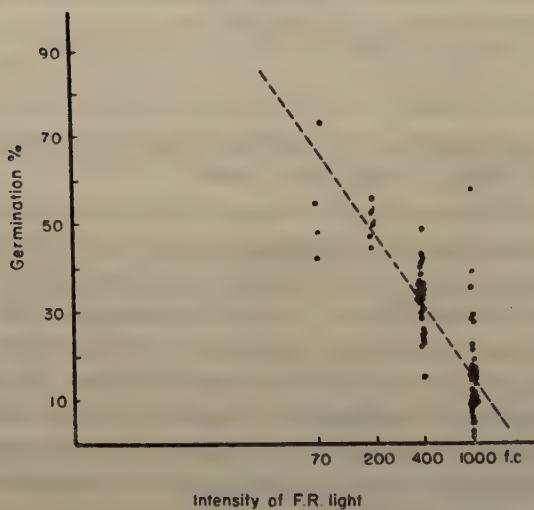


Figure 11

The effect of F.R. intensity on the response of *Amaranthus retroflexus* seeds to stimulating illuminations. The seeds were kept at 37°C for 2 days in continuous F.R. of different intensities, then illuminated with 3×10^3 f.c. sec of white light and subsequently transferred to darkness. Germination was estimated 2 days later. Seedlings which germinated in continuous F.R. (initial germination) were removed before the illuminations (cf. Figure 10).

TABLE V

*Effect of continuous blue and F.R. light on the response of *Amaranthus retroflexus* seeds to short white illuminations*

The seeds were sown in continuous light under different filters; light intensity was 1000 f.c. temperature 37°C. After 2 days the seedlings were removed and the remaining seeds illuminated with 60×10^3 f.c. sec of white light, then transferred to darkness

Colour of filter	Colour of light transmitted	Initial germination (by end of light period)	Germination after white illumination***
Blue + red	F.R.	25±5	8±4
Blue	F.R. + blue	22±3	14±4
Blue + sol.**	Blue	49±6	68±10
Dark control	—	49±10	92±4

* There was no germination in control lots that were transferred to darkness without illumination.

** 2 cm $\text{Cu}(\text{NO}_3)_2$ solution.

*** % of illuminated seeds.

From Figure 10 it may be seen that somewhere between 22–70 f.c. saturation was reached in regard to F.R. inhibition of the initial germination. As to the effect of F.R. on the responsiveness to red light, continuous F.R. illumination of as low an intensity as 2 f.c. was enough to cause a significant reduction in the response (Kadman-Zahavi 1959). On the other hand, saturation was not reached even at 1000 f.c. (Figure 11).

Source of light and temperature

When white fluorescent light was used instead of incandescent light there was no inhibition at 37°C, but at 26°C strong inhibition was evident. At this temperature, when the red was cut out of the fluorescent light by wrapping the dishes with blue cellophane, initial germination was entirely inhibited and the response to a short illumination was reduced considerably (Kadman-Zahavi 1959). This indicated that the small amounts of F.R. generated in fluorescent lamps should not be overlooked, especially with prolonged periods of illumination (see also Stolwijk and Zeervaart 1955; and Wassink *et al.* 1957).

It may be seen from Figure 10 that at 37°C the initial germination of some seed was not inhibited by F.R. of any intensity. However, at 26°C there was no germination of *A. r.* seeds in continuous F.R. even at the intensity of 2 f.c. (Kadman-Zahavi *et al.* 1957). This showed that under certain conditions all the seeds could be affected by F.R.

DISCUSSION

Three inhibitory effects of F.R. on the germination of *A. retroflexus* seeds have been demonstrated.

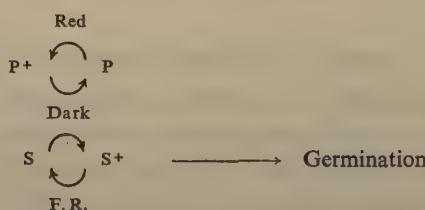
One, the well known reversible red-F.R. effect which has been described by Borthwick *et al.* (1952) for other seeds. This will henceforth be called: *The reversible effect of F.R.*

A second effect of F.R. was the inhibition of the initial (or dark) germination. There are some indications that this inhibition may be caused by the reversible effect of F.R. Jones and Bailey (1956) have shown that in *Lamium. amplexicaule* seeds a short F.R. illumination was enough to cause a strong inhibition of the dark-germination and that a subsequent red illumination completely reversed this inhibition. There is indirect evidence that the case of *A. retroflexus* seeds may be similar (Kadman-Zahavi 1959), but no further work has been done on this subject.

The third effect of F.R. is that which prevents the seeds from responding to subsequent red illumination. This effect of F.R. was manifested only after prolonged application; it was not reversed by red light but it was cancelled by a slow dark reaction. Henceforth this effect of F.R. will be called: the effect of *prolonged F.R.*

The action of the reversible effect of F.R. It has been shown (Figure 3) that short F.R. was most effective at some time interval after the red illumination. The optimum length of this interval depended on temperature. This indicated that F.R. did not reverse the action of the red light directly but affected some dark-reaction that was initiated by the red illumination.

The action of the R and F.R. may be represented by the following scheme:



A short *red* illumination converts the red pigment (P) into an activated state (P+). In a *dark* reaction the activated pigment acts on a substance (S) and converts it into an activated state (S+), while being itself converted back into its original state (P). In the activated state the substance (S+) promotes germination. A short F.R. illumination converts the activated substance (S+) into its original state (S), thus nullifying the effect of the red illumination. The reaction is completely reversible, as at the end of the F.R. phase the participating substances are in their original states: (P) and (S).

The action of prolonged F.R. The reduction of the sensitivity of the seeds to red prolonged F.R. could be caused either by a direct effect on the above system or it could be an indirect effect of a more "general inhibitory" action. A detailed investigation of this problem has not yet been undertaken; but preliminary experiments seem to indicate that prolonged F.R. illumination acts directly on the system involved in the R-F.R. reactions. It could do this either (1) by changing the substance (S) in a way that prevents its activation, or (2) by altering the red pigment (P), or else (3) by interfering with the utilisation of the activated substance (S+) in subsequent reactions. But even without understanding its mechanism of action, the demonstration of the prolonged F.R. effect may explain several effects of light on seed germination. Thus we may suggest that most of the photoperiodic effects on germination (Isikawa 1954) may be caused by the above mentioned effects of light and darkness: F.R. inhibition of the initial germination, the stimulation of germination by red light, the reversal of this stimulation by short F.R., the reduction of responsiveness to red by prolonged F.R. illumination, and the recovery of this responsiveness by a dark-reaction.

It is probable that in different seeds the relative rates of these reactions may be different. These may change even in the same seed with change of age or of temperature (Kadman-Zahavi 1959). There may also be cases in which recovery of the sensitivity to red light cannot be attained either because the dark-reaction is too slow or for other reasons. In these cases, the seeds become "light-dormant" (Evenari 1956).

It is now well established that apart from seed germination, the reversible R-F.R. system is also effective in plant elongation, in photoperiodic effects on flowering as well as in other morphogenetic phenomena (Toole *et al.* 1956; Wareing 1956; Wassink and Stolwijk 1956; Liverman 1955; Van der Veen and Meijer 1958; and others). It is still to be determined whether the prolonged F.R. effect is also active in the above mentioned phenomena. Recent investigations with internode elongation indicate that this may be the case (Van der Veen and Meijer 1958; Meijer 1959; Sale and Vince 1959). In these investigations it was found that under certain conditions red light had the same effect as F.R. light. In these investigations fluorescent light was used as source for red light. This light includes 2% or more of F.R. This F.R. may be active in the prolonged F.R. effect, as it has already been shown that for *A. retroflexus* seeds the cumulative effect of such small amounts of F.R. when applied for prolonged periods may have very strong inhibitory effects on the sensitivity of the seeds to red light. It is also possible that the pigment involved in the prolonged F.R. effect may have some absorbance in the range below 700 m μ .

If the prolonged F.R. effect operates in green plants, then this may form a mechanism by which the reactions of the plants to light can be changed during the time of exposure. At the beginning of an illumination period the red reaction may predominate but with prolongation of the exposure this may change until a stage is reached

sensitivity to Red

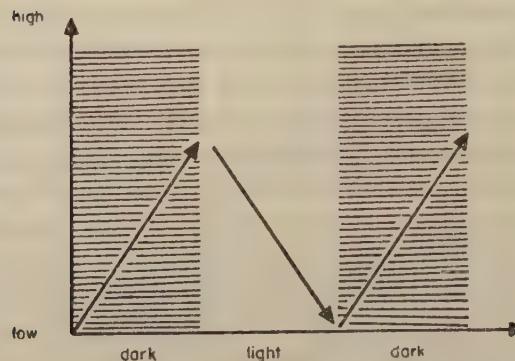


Figure 12

Schematic representation of the change in sensitivity of *Amaranthus retroflexus* seeds to short white illumination when placed alternatively in light and darkness.

in which red has no effect. During the dark period sensitivity to red light may be recovered again. This is schematically represented in Figure 12.

The rates of the prolonged F.R. and the Dark reactions may differ greatly in different plants and may be responsible for the different critical intensities described by Meijer (1959). The prolonged F.R. reaction may also be involved in the photo-periodic reactions of flowering as well as in many other formative phenomena.

This investigation was carried out under the guidance of Prof. M. Evenari. I wish to thank him for his interest and help.

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STUDIES ON THE ORIGIN OF CULTIVATED BARLEY

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ABSTRACT

The adaptive specialization in seed dispersal in the wild relatives of cultivated barley has been investigated. This specialization has been recognized as a characteristic evolutionary trend in the genus *Hordeum*. The ensemble of spikelet and ear characters associated with the wild mode of seed dispersal is described and its adaptive value pointed out. Realizing the breakdown of this adaptive specialization under domestication, an attempt has been made to employ the information on the dispersal mechanism as a means for assessing primitiveness or wildness of characters as against derived characters which could have evolved only under the impact of domestication.

Spontaneous hybridization between *H. spontaneum* and six-rowed *H. vulgare* was studied. Hybrid swarms were found to be confined to disturbed habitats and to consist of a whole range of intermediates, among them various brittle hexastichous forms.

The conclusion was arrived at that the two-rowed condition in wild *Hordeum* species reflects an adaptive specialization in seed dispersal and that this specialization evolved already geologically long ago, at the very start of the differentiation of this genus. At the beginning of agriculture the section *Cerealia* of the genus *Hordeum* was most likely represented only by distichous types. Establishment of six-row mutants has been possible only under domestication, after the wild mode of seed dispersal was drastically altered by man. Hexastichous brittle barley types (such as the various *agriocirthon* and brittle *intermedium* forms) cannot be regarded as ancestral types. They are only secondary hybrid derivatives.

The origin of cultivated barley is explained on basis of a "two-row" model and *H. spontaneum* is regarded as the sole ancestor of all cultivated barley forms. The mode of origin and the trends of alterations of barley under domestication are discussed. West Asia is regarded as the place of origin of barley cultivation.

INTRODUCTION

Early students of the origin of cultivated barley (De Candolle 1884, Körnicke 1885) regarded the wild two-rowed *Hordeum spontaneum* Koch (= *H. ithaburense* Boiss.) as the progenitor of cultivated barley. However, already De Candolle advanced an alternative hypothesis, namely, that the six-rowed cultivated barley could have originated from an unknown six-rowed wild ancestor.

In the last thirty years the "six-row" hypothesis has been vigorously advocated by Schiemann (1932, 1948, 1951). Schiemann regarded the staminate, lateral spikelets of the two-rowed barleys as degenerated organs and argued that theoretically it is improbable that such reduced parts could have re-evolved into fertile spikelets. He concluded that a wild, six-rowed prototype must have existed in historical times and have given rise to the six-rowed cultivated barley.

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The six-row hypothesis received what seemed its final verification when Schiemann's hypothetical brittle six-rowed type was actually found in barley collections brought from Tibet. This form was described by Åberg (1938, 1940) as a new wild species, *Hordeum agriocirthon*, and since that announcement barley students have generally accepted the six-rowed prototype as a reality. There are few notable exceptions (e.g. Bakhteyev 1947, 1953, Helbaek 1959), but most of the recent attempts to explain the origin and variation in cultivated barley, such as made by Schiemann (1948, 1951), Åberg (1940), Freisleben (1940), Takahashi (1955) and Hoffmann (1959), are all based on such an assumption. The various phylogenetic schemes advanced by these authors propose a six-rowed wild prototype either as the starting step for all cultivated barley forms, or at least assume such an ancestry for the cultivated six-rowed varieties.

In a previous note (Zohary 1959) the present author presented evidence to suggest that *H. agriocirthon* is not a genuine wild species but rather a secondary hybrid derivative, the product of spontaneous hybridization between wild two-rowed *H. spontaneum* and cultivated six-rowed barley. In that note the conclusion was also arrived at that the whole concept of a six-rowed wild progenitor is hardly acceptable, and that all cultivated barley forms have most likely evolved from a two-rowed wild progenitor.

The aim of the present paper is to further support the hypothesis that two-rowed wild *Hordeum spontaneum* is the likely ancestor of all cultivated barley forms and the only genuine, or primary wild species in the section *Cerealia* of the genus *Hordeum*. Support for this view has been drawn mainly from two lines of evidence which up to now have largely been neglected by barley students.

First, the seed dispersal biology of *H. spontaneum*, as well as of other wild *Hordeum* species, was examined and an attempt was made to recognize the ensemble of morphological traits associated with the wild mode of fruit dissemination. Botanists have already stressed the fact (see Stebbins 1950, 1956) that specialization in dispersal mechanisms has been of major evolutionary importance in the grass family. Moreover, the morphology of the spikelet and inflorescence in many genera of *Gramineae* largely reflects their particular adaptation in fruit dissemination. The wild *Hordeum* species are also specialized in this respect and have a wedge-type mechanism which inserts their fruit in the ground. Domestication obviously brought a drastic change in this adaptive specialization. An understanding of the details of seed dispersal under natural conditions, and in particular the recognition of spikelet and ear characteristics associated with that function, offers us, therefore, a sensitive working tool, with the help of which one can evaluate the morphological traits in the *Cerealia* group which should be considered wild or "primitive" as against those characteristics which should be regarded as derived under domestication.

A second line of attack was the examination of natural hybridization between *Hordeum spontaneum* and the cultivated six-rowed barley. Wild and cultivated forms in the *Cerealia* group are all interfertile. They are reproductively isolated from one

another only by ecological barriers and by virtue of their system of self-pollination. Secondary hybrid combinations can therefore be expected to be produced occasionally. As a result of the mating system such hybrid derivatives can establish themselves as truly breeding lines in a relatively short time. They can easily be mistaken for "primitive forms" and be erroneously considered "ancestral types". Information on the occurrence of natural hybrid swarms, the types of recombination forms found in them and the habitats where such hybrid derivatives are able to survive, can contribute in avoiding pitfalls connected with secondary hybrid derivatives in consideration of the origin of cultivated barley.

DISTRIBUTION OF WILD AND CULTIVATED BARLEY IN ISRAEL

Six-rowed *Hordeum vulgare* is extensively cultivated in Israel. Barley constitutes one of the most important winter crops in central and northern Israel and is included in the various schemes of crop rotation practised here. At present, several tested varieties constitute the bulk of barley cultivated in this country. All of them are awned, hexastichous, with semi-dense awned ears. Most wide-spread are the varieties "Glacier", "Nissanit", "Beecher" and "Arivat".

Local two-rowed barleys as well as several native six-rowed varieties with a comparatively low yield have been almost completely discarded by modern farmers. They are met with at present only as relicts in the less developed rural areas or are occasionally found contaminating uncertified barley seed.

Wild *H. spontaneum* is a common component of the open, herbaceous dwarf shrub formation and the semi-steppe vegetation which dominate considerable stretches of the hilly area of northern and central Israel. In addition to occurring in these open, herbaceous formations, *H. spontaneum* is also fairly common in areas with a typical Mediterranean dwarf shrub ("Batha") vegetation. Here, however, this barley is restricted to sites recently cleared of their shrubs as well as to edges of cultivation and to recently abandoned fields. *H. spontaneum* is particularly common in the eastern Galilee and in the western foothills of the Judean Mountains. Most of the observations reported in this paper were made in these districts.

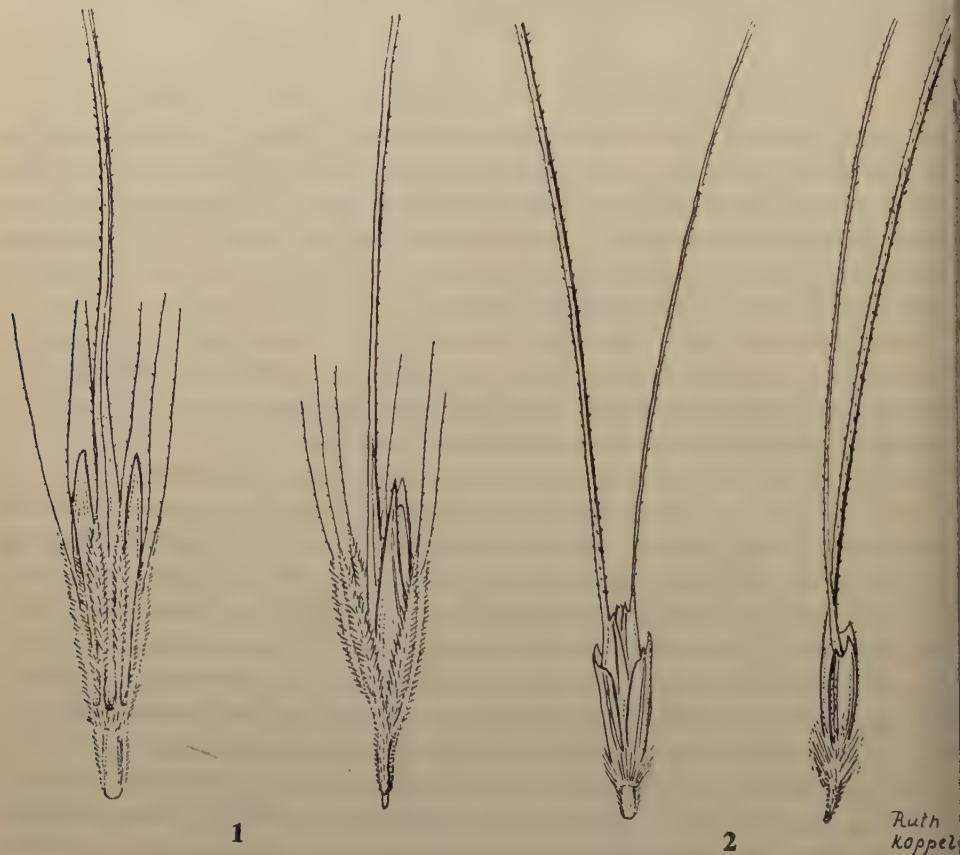
Contacts between barley cultivation and *H. spontaneum* are common; they occur mostly in the mountainous districts of Israel and in the foothills, where cultivation in patches or restricted to valleys, and where stands of *H. spontaneum* occupy the adjacent hillsides and grazing areas.

SEED DISPERSAL

The seed of *H. spontaneum* ripens in Israel in late April and early May, at the end of the rainy season. After ripening, the ears of this annual grass disarticulate, and the pointed, arrow, arrow-like, one-seeded triplets (see Figure 1) fall head down to the ground. A considerable number of these triplets become firmly anchored in the ground, either among the drying stalks and organic residue of the previous year's growth or in soil

cracks and among stones. The summer aspect of *H. spontaneum* is characterized by dry stands of the previous generation (or what is left of them after summer grazing) with the dispersal triplets stuck vertically in the ground, and with only the stiff long awns protruding from the soil.

Mechanically the triplet (see Figure 1) is adapted to insertion into the ground (trypanocarpy according to the classification of M. Zohary, 1937). It is a wedge or arrow-shaped ("Keilfrucht") dispersal unit; the sharp-pointed internode of the rachis



Figures 1-2

Dispersal units of 1. *Hordeum spontaneum*; 2. *Triticum boeoticum* (both in front and side-view).

Note the similarity in arrow-like structure in the two genera.

serving as the tip of its arrow-head, while the stiff staminate lateral spikelets, serving as arrow-wings, resist any back movement effectively. Resistance to back movement is provided also by the upward directed hairs occurring on the lower part of glumes and on the edges of the rachis, as well as by the scabrous surfaces of lemmas, glumes

and awns. The fact that the long stiff awns vibrate continuously in the wind is noteworthy. This motion apparently also assists the triplet to penetrate the ground.

Several suggestions can be advanced as to the adaptive value of this mode of seed dispersal. The first obvious fact is protection from extreme desiccation during the hot summer. Another advantage is protection of the seed from grazing and seed collecting animals, such as sheep, rodents and ants. The activity of ants should not be underestimated. Nests of the social harvester ant *Messor semirufus* are almost universally found in the open herbaceous vegetation in which *H. spontaneum* grows. These ants (personal communication by U. Nur) systematically clean the ground of buried fruit. They cut the awn of each triplet at its base and carry the rest of the fruit to their nests. However, they are not able to pull out fruit which has been buried in the ground.

The effect of summer fires is another factor to be considered. Such fires are of frequent occurrence in the open semi-steppe and dwarf shrub vegetation. Several burned stands of *H. spontaneum* were examined at the beginning of the growing season of 1958-1959. As expected, only well buried triplets germinated. Fruit which did not penetrate beyond the tips of the lateral spikelets was scorched and failed to germinate.

Fruit burial is of advantage also at the start of germination. The vertical position of the inserted dispersal unit offers proper orientation for the plumule and radicle. Apart from this advantage one has also to consider the climatic conditions prevailing at the start of germination. Rainless dry spells between the first effective autumn rain and subsequent ones are of common occurrence in the Middle Eastern countries. Under such weather conditions unburied fruit is apt to suffer considerable desiccation just after the initiation of germination, while inserted seed enjoy continuous humidity. Repeated observations made at the beginning of the growing seasons of the years 1957 and 1958 fully confirmed this view. Two or three weeks after the first effective rain, seedlings from buried fruit were more advanced in their development than those that had germinated on the surface. The autumn of 1958 was especially indicative. In that year there was an interval of several weeks between the first rain and subsequent ones. While it was observed that almost all the seedlings from scattered unburied fruit dried up and died during that dry spell, most of those which germinated from buried fruit survived.

Another fact that should be stressed is the wide occurrence of trypanocarpy, or fruit insertion, in the regions and habitats where *H. spontaneum* grows. This fact has been stressed already by M. Zohary (1937). Wedge-shaped fruit and drill fruit are a characteristic feature of the Middle Eastern herbaceous and steppe vegetation. A most striking resemblance to the wedge-shaped dispersal unit of *H. spontaneum* is found for example in the wild wheats *Triticum dicoccoides* and *T. boeoticum*. Here, too, the ripe ears break up into arrow-like units (see Figure 2). It should be pointed out, however, that the dispersal units in *Hordeum* and *Triticum* are only analogous.

While in the wild barley the lateral spikelets function as wings of the arrow-head, in the wheats this role is performed by the stiff glumes.

Additional examples of trypanocarpy are found in various other Middle Eastern species of the genus *Hordeum* (e.g. *H. bulbosum*) as well as in several other common grasses such as *Avena sterilis*, *A. barbata*, *Bromus sterilis*, *Stipa tortilis*, *Aegilops sharonensis*, *Ae. ligustica* and *Secale montanum*.

All these observations indicate that one has to consider the triplet of *Hordeum spontaneum* as a specialized dispersal device. Its morphology, including the shape of the sterile lateral spikelets, has long since been determined by natural selection and should be considered as an adaptation to the wild environment. In fact most of the diagnostic characters used by barley taxonomists to distinguish *H. spontaneum* from cultivated barley are associated with this adaptation.

HYBRIDIZATION

Methods

The Anderson (1949) technique of pictorialized scatter diagrams was employed to obtain a clear picture of the patterns of variation found in the hybrid swarms and for their comparison with pure populations of *H. spontaneum* and cultivated barley. Herbarium specimens were placed with the herbarium of the Hebrew University of Jerusalem. The following morphological traits were selected for the analysis of population samples (see also Figure 4). Only mature ears were scored, and as a rule the sixth lowest triplet in the ear was used for comparison of spikelet characteristics.

Awns of the lateral spikelets: Lateral spikelets in *H. spontaneum* are awnless, while in all six-rowed cultivated barley varieties in Israel the lateral spikelets have awns as long or almost as long as those of the median spikelets. The ratio: length of the median spikelet (length in mm of its palea) to length (in mm) of the left lateral spikelet awn was used to express the relative size of the lateral awn (see ordinates in Figures 3, 5). In the case of awnless lateral spikelets, the denominator was given the value of one unit.

Spreading of lateral spikelets: The lateral spikelets in *H. spontaneum* are appressed to the median spikelets, while in *H. vulgare* they are widely spreading. The ratio: length of the median spikelet (awn excluded) to distance between the tips of the two lateral spikelets of the triplet was used to express this trait (See abscissae in Figures 3, 5).

Disarticulation of the rachis: A plant was classified as brittle, whenever its ripe ear disarticulated upon bending or slight stretching, and when the disarticulation point showed a smooth scar. It was noted, however, that several of the intermediates which were classified as brittle disarticulated less easily than did typical *spontaneum* ears.

Fertility of lateral spikelets: Plants were classified as intermediates, whenever one to several lateral spikelets in the ears were filled. In such cases the fertile lateral spikelets were usually found in the middle part of the ear.

Width of lateral spikelets: While in *H. vulgare* the lateral spikelets are similar in width to the median ones, in *H. spontaneum* they are considerably narrower. A scale of five grades (see Figure 4) was employed to analyse this trait.

Length of the rachilla: The length of the rachilla of the median spikelet (hair excluded) was measured to the nearest mm. A scale of four grades was employed (see Figure 4).

Hairiness of rachis, glumes and rachilla: A scale of five grades of hairiness was used to score the density of hair cover, starting from the relatively very sparsely covered *H. vulgare* to the very densely hairy *H. spontaneum*.

Fusion of the outer glume: In *H. spontaneum* the base of the external glume in each lateral spikelet is partly fused to the spikelet peduncle. A scale of three grades was employed in the scoring of this trait. It is noteworthy that the Israeli cultivated varieties do not exhibit such a fusion, and that peduncles in these varieties are shorter.

Distribution and Nature of Hybrid Swarms

Swarms of hybrids between cultivated six-rowed *H. vulgare* and wild *H. spontaneum* have been repeatedly encountered in Israel in the last four years. Several dozens of such swarms have been examined. They usually contain an entire range of intermediates and recombinants between these two species (see Plate I). Most hybrid colonies were found on sites where stands of *H. spontaneum* grow in close proximity with cultivated barley. As in many other cases of interspecific hybridization (Anderson 1953) such swarms were found to be ecologically restricted only to places that had been greatly disturbed by man, and to exhibit a characteristic sporadic distribution. Hybrid swarms were particularly easy to locate in the hilly district of eastern Galilee and in the Judaean foothills where *H. spontaneum* is an important component of the herbaceous steppe-like vegetation covering the hillsides and where, due to topography, cultivation is necessarily in patches. Contacts in such regions are numerous, and hybrid swarms were easily detected if only looked for in their proper habitats. They are almost always found in close proximity with pure *H. spontaneum* populations which occupy the adjacent undisturbed hillsides. The main localities in which hybrid swarms were observed in Israel are shown on the accompanying map. Descriptions of the locations are given in Table 1.

The habitats in which hybrid swarms occur can be roughly divided into the following groups:

(1) Roadsides and margins of cultivated fields: Ditches along roadsides and tracks at the edges of fields are apparently one of the most favourable niches for hybrid swarms and for highly introgressed populations of *H. spontaneum*. The ditches and the edges of roadsides in Israel are usually hoed and cleared of their vegetation every summer as a precaution against fires, while the field margins are disturbed by

TABLE I

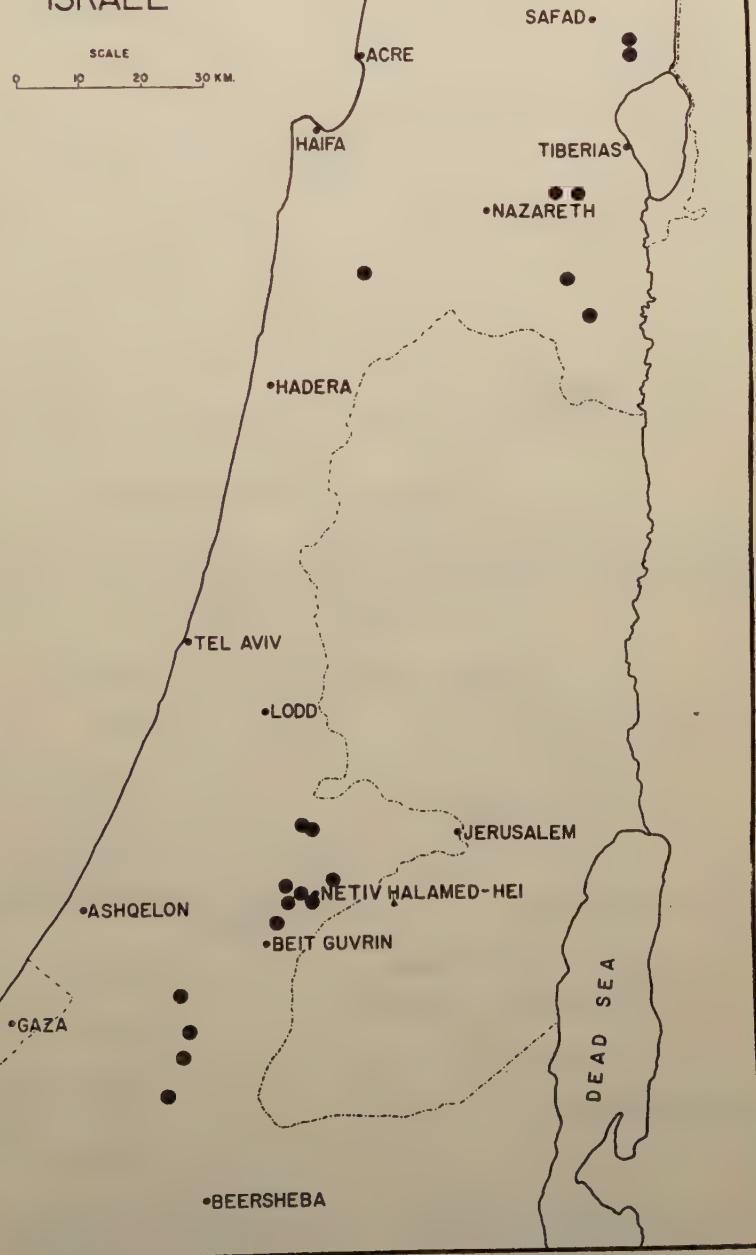
Localities and nature of hybrid swarms observed in Israel

Locality	Nature of swarms and time of observations
1. 1 km east of Sdeh-Boker, approx. 45 km south of Beersheba.	Neglected cultivated patch in a wadi bed (1956).
2. Between Pelugot and Beit Kamma on Rehovot-Beersheba road.	Several hybrid swarms sporadically distributed along roadsides (1957).
3. 6 km north of Beit-Guvrin, Judaean foothills.	Hybrid swarm in a strip of abandoned cultivation along barley field; hybrid derivatives as weeds in nearby fields (1958).
4. Netiv Halamedhei settlement, Judaean foothills.	Several hybrid swarms observed in the settlement's area: a) in abandoned fields; b) in ditches along roadsides; c) in edges of cultivation as "weeds" in wheat, barley and oat fields (1957, 1959).
5. 1 km south of Kefar Zekhariya, Judaean foothills.	Two hybrid swarms along road ditch (1959).
6. 4 km west of Hartuv on Jerusalem-Tel-Aviv road, Judaean foothills.	Hybrid swarm along roadside (1957); largely replaced by pure <i>H. spontaneum</i> (1958).
7. Approx. 2 km north of Daliya settlement, Samaria hills.	Hybrid swarm along roadside (1959).
8. Between Kefar Tabor and Beit Keshet, Lower Galilee.	Hybrid swarm along roadside (1957).
9. Approx. 5 km north of Ein Harod on road to Moledet, Lower Galilee.	Hybrid swarm at edge of cultivated field (1957).
10. 1 km south of Ammiad settlement, Eastern Galilee.	Several hybrid swarms along margins of cultivated fields and in abandoned cultivation. Hybrid derivatives as weeds in fields (1957).

farm machinery every now and again. Hybrid colonies were found to occur sporadically along such ditches and roadsides. A characteristic feature of the colonies found was their abrupt replacement by pure stands of *H. spontaneum* in the adjacent undisturbed areas—only a few metres away. Hybrid colonies in road ditches and on the fringes of cultivation seldom attain population sizes of more than several thousands of individuals. They usually consist of a majority of *spontaneum*-like plants, some intermediates with semi-fertile lateral spikelets (see Plate I, nos. 4,6,7,14,16), as well as *agriocritthon*-like forms (see Plate I, nos. 8,9,10,11). Usually some *vulgare*-like plants are also met with here, sometimes together with a number of true *vulgare* escapees. A typical example of such a hybrid swarm is presented in the pictorialized scatter diagram in Figure 5 top. The range of intermediates and recombinants en-

LOCALITIES OF HYBRID SWARMS IN ISRAEL

SCALE
0 10 20 30 KM.



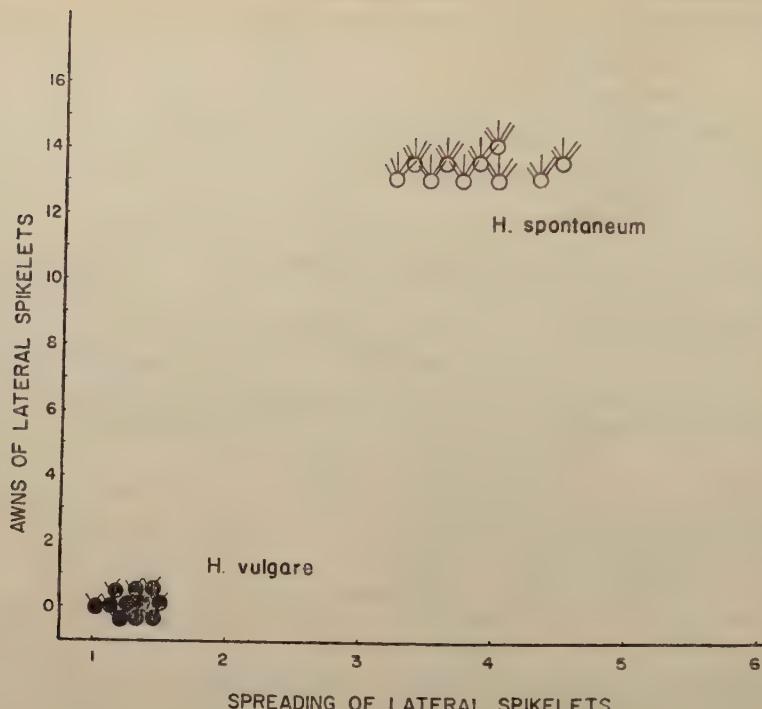


Figure 3
Pictorialized scatter diagram comparing *Hordeum spontaneum* growing on undisturbed hillsides at Netiv Halamedhei, Judaean foothills, with cultivated six-rowed *H. vulgare*, variety "Glacier", growing in nearby field.

Figure 4
Explanation of symbols used in scatter diagrams

1. Disarticulation of rachis

- brittle rachis
- non-brittle rachis

2. Fertility of lateral spikelets

- all lateral spikelets sterile
- lateral spikelets semi-fertile
- all lateral spikelets fertile

3. Width of lateral spikelets

- less than in *H. spontaneum*
- spikelet shrunk as in *H. spontaneum*
- slightly inflated
- much inflated
- similar to median spikelet

4. Length of rachilla

- 5.0 mm or more
- 3.0-5.0 mm
- 1.5-3.0 mm
- 1.5 mm or less

5. Degree of hairiness of rachis, glumes and rachilla

- very dense
- dense
- medium
- slight
- very slight

6. Degree of fusion of external glume base with spikelet penduncle

- fusion extending over 2.5 mm or more
- slight fusion
- glume base free

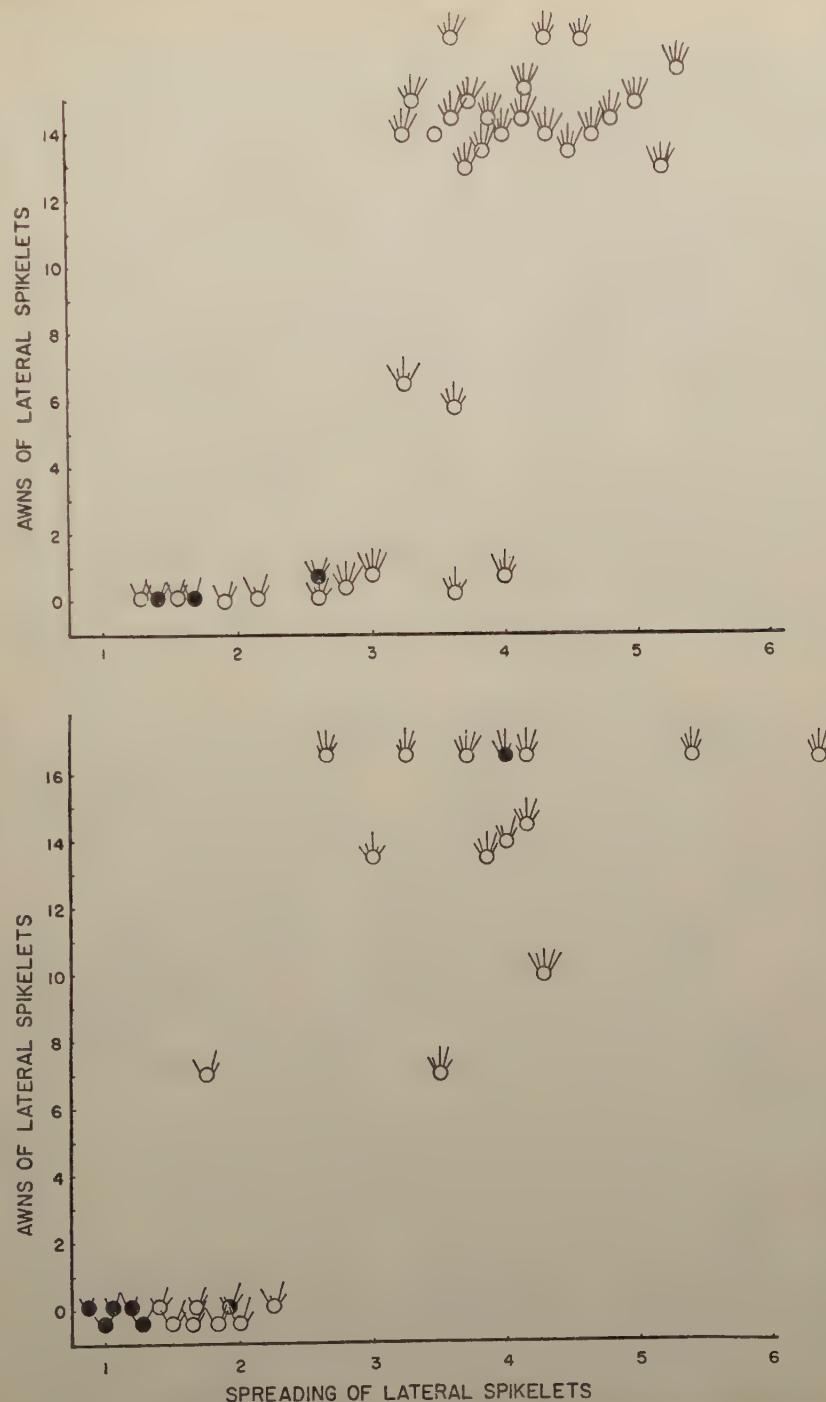


Figure 5

Pictorialized scatter diagrams of two hybrid swarms at Netiv Halamedhei, Judaean foothills. Upper diagram represents swarm in road ditch; lower diagram: swarm in cultivated field.

countered in that swarm is shown in Plate I. This particular population sample was taken in a road ditch opposite the settlement of Netiv Halamedhei, Judaean foot-hills. For comparison, samples of pure *H. spontaneum* and cultivated *H. vulgare* from the same area are represented here too. Their scatter diagrams are shown in Figure 3. The *H. spontaneum* sample was taken from a stand growing on an undisturbed hillside adjacent to the hybrid swarm, and the cultivated barley from a nearby field.

(2) Abandoned fields: Fields sown with barley and then left unploughed for a number of years form another group of habitats which harbour hybrid swarms. Here hybrid colonies are met with sporadically, usually also in close proximity with pure stands of *H. spontaneum*. As a rule one finds a wide range of intermediates mingled with cultivated barley escapees on these sites. It is, however, the impression of the present author that the population structure in such fields changes relatively rapidly, and that hybrid recombinants here become swiftly replaced by the better adapted true *H. spontaneum* individuals, as well as by other pioneer annual grasses such as *Avena sterilis*. After more than 5 years of abandonment these fields are usually completely occupied by the latter.

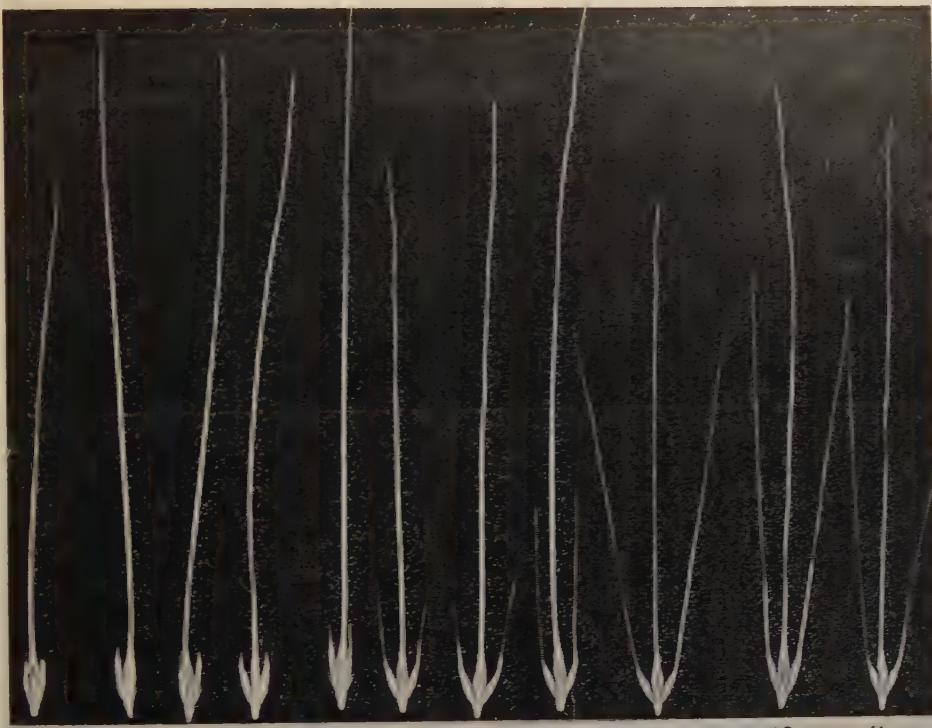
(3) "Weeds" in cultivated fields: Hybrid derivatives are sometimes found also as "weeds" among winter cereals such as wheat, barley, oats, etc. Such intermediates usually occur where hybrid swarms are present also in road ditches or field margins in the same vicinity.

The scatter diagram of a representative sample of a hybrid swarm from a cultivated field is shown in Figure 5, lower diagram. The large number of *H. vulgare* escapees still found in this sample is noteworthy.

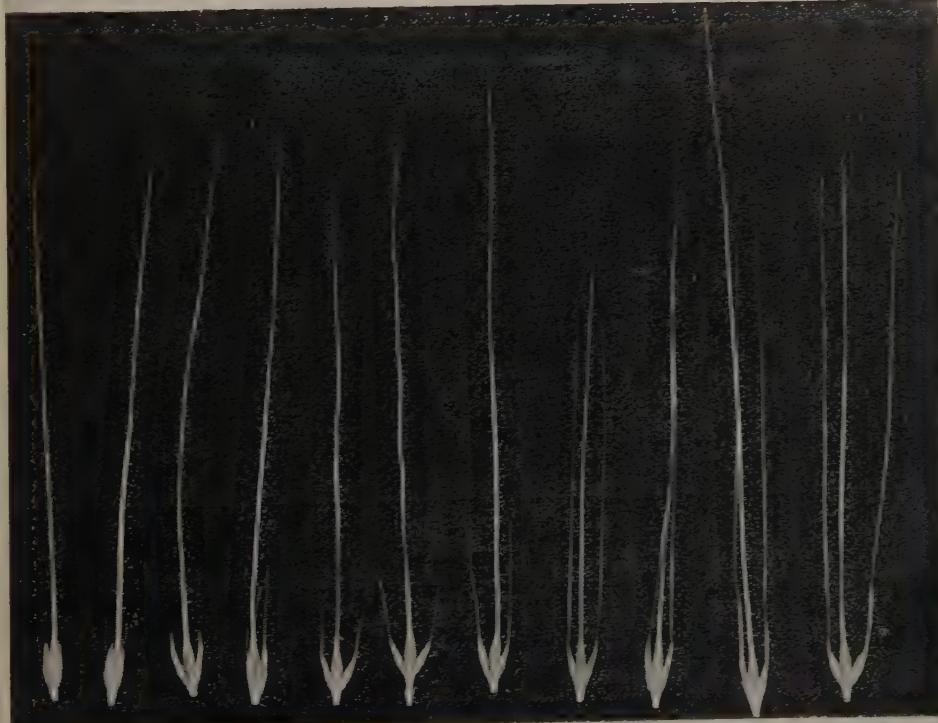
Characteristically, the picture in such fields is different from that in the less "domesticated" habitats of road ditches or abandoned fields. A large proportion of intermediates growing as "weeds" in fields are various brittle *agriocrithon*-like forms as well as *intermedium* types. Another feature is a lesser continuity in the range of variation among the hybrid derivatives growing in a given field; commonly one encounters here a prevalence of one or few types. This fact might indicate the partial establishment of stable, more homozygous lines in such fields.

Progeny Tests

In 1958-59 the progeny of about forty intermediate plants collected in various hybrid swarms was raised and tested (Miss T. Tovia, unpublished M. Sc. thesis, The Hebrew University). A full account of these progeny tests will be published elsewhere. As expected, several of the intermediates bred almost true (regarding their more conspicuous morphological characteristics), while others proved to be quite heterozygous with their progeny showing a wide range of segregation. An example of such segregating progeny is shown in Plate II. They furnish further evidence as to the hybrid nature of the material investigated.



1 2 3 4 5 6 7 8 9 10 11



12 13 14 15 16 17 18 19 20 21 22

Plate I

Representative sample of intermediates encountered in a hybrid swarm at Netiv Halamedhei, Judaean foothills. Upper row: triplets taken from plants with brittle ears. Lower row: triplets from plants with non-brittle ears.

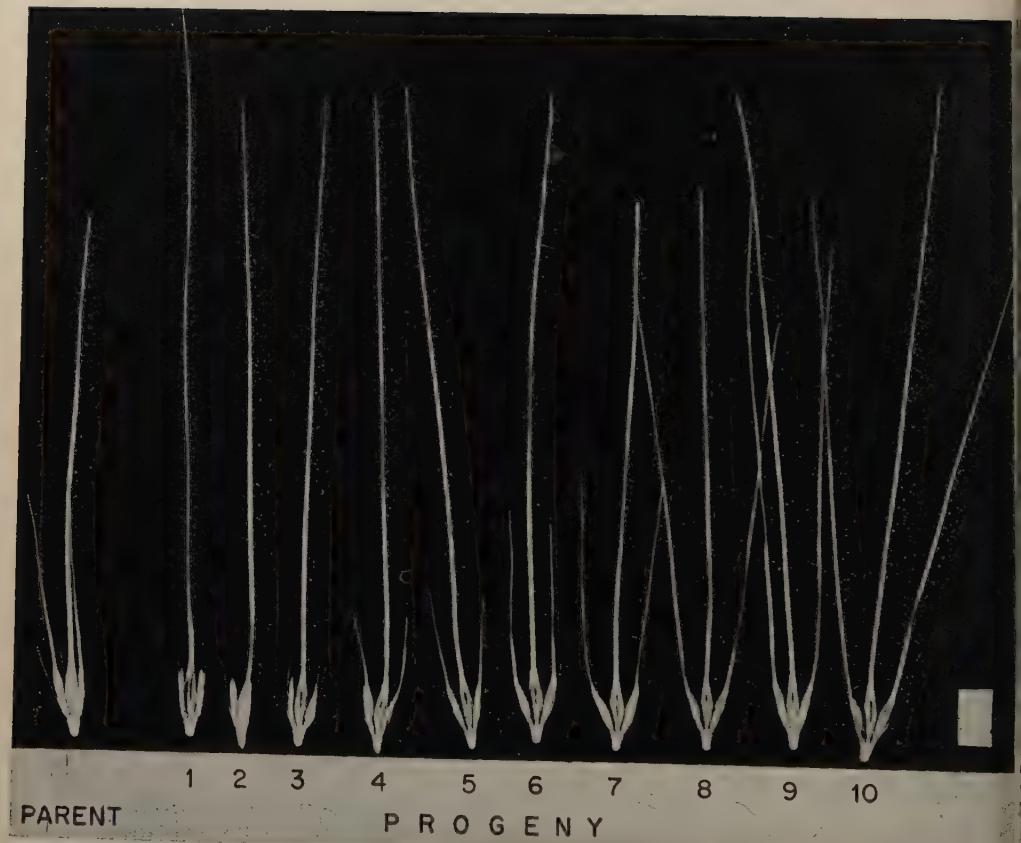


Plate II

Segregation in progeny of natural intermediate *agriocirthon*-like plant (on left); all segregants are brittle.

DISCUSSION

Secondary Hybrid Derivatives

As already concluded in a previous note (Zohary 1959) the six-rowed brittle barley forms described by Åberg as *Hordeum agriocrithon* can no longer be regarded as a genuine or primary wild species. They are most likely secondary hybrid derivatives, the result of spontaneous hybridization between *H. spontaneum* and cultivated six-rowed *H. vulgare*. Such forms are apparently repeatedly produced among other hybrid recombinations in places where these two species occur sympatrically. Their relative rarity should be attributed to the fact that they are ill-adapted to disseminating their seed and to maintaining themselves under truly wild conditions.

The question still left open is whether *agriocrithon* types are always relatively short lived hybridization products, or whether such recombinations have been successful in some areas in establishing themselves as ecologically stable forms. In Israel, such hybrid derivatives face a precarious existence in the rapidly changing disturbed habitats. Whether this is always the situation elsewhere is yet to be investigated.

A yet unsolved problem is the nature of the *agriocrithon* material brought from Tibet. It is the present author's view that the Tibetan material is similar in nature to the Israeli forms and has, in all likelihood, evolved from recent hybridization between six-rowed cultivated barley and *H. spontaneum*. An obvious difficulty in this assumption is the lack of records on the occurrence of *H. spontaneum* in Tibet. But this could be attributed to the poor botanical exploration of that area, and it is still very probable that *H. spontaneum* does actually expand as far east as Hindu-Kush and Tibet.

Even if it is assumed that *H. spontaneum* does not exist in Tibet, *agriocrithon* types there can still be regarded as being of hybrid origin. Their occurrence in Tibet could be due to their transport to that country by man from Western Asia. In Iran and Afghanistan *H. spontaneum* is known to exist, and hybridization could have taken place there. In this case the Tibetan *agriocrithon* types should be ecologically well established by now and should be more stable than their Israeli counterparts. But whatever the origin of the Tibetan *agriocrithon*, there is no evidence of its survival under truly wild conditions. All we know is that the *agriocrithon* material from Tibet was separated from seed samples of cultivated barley. It is therefore safe to assume that these plants were growing as weeds in cultivated fields, i.e. in secondary habitats. Unless evidence to the contrary is brought forward, they cannot be regarded as truly wild primary forms.

In the same category with *H. agriocrithon* one has to place the numerous other recombination types encountered in hybrid swarms between *H. spontaneum* and cultivated barley. Such intermediates (see Plates I and II) are also apparently relatively ill-adapted to maintain themselves under wild conditions and survive only precariously in intermediate or disturbed habitats. Yet when a favourable niche is

available for even a few generations, more or less true breeding lines can be expected to evolve by virtue of the breeding system of self-pollination. Conspicuous among such secondary hybrid derivatives is the group of brittle *intermedium* forms which includes both true breeding and segregating lines (see Plate I, upper row). Such forms have already been described in Israel by Kamm (1954). From Kamm's data and from personal communication with him it can be concluded that his material is essentially identical with the *intermedium* types found in the hybrid swarms examined by the present author.

Of similar secondary hybrid origin are most likely the several West Asiatic "primitive" or "linking" forms described by various authors (for review see Schiemann 1948). One can easily match these forms with similar plants among the wealth of segregants encountered in the hybrid swarms. The genuine relic status of any of these odd forms is highly questionable. Unless convincing circumstantial evidence is provided to support such an assumption, it is much safer to regard them, too, as secondary products of occasional hybridization.

The Wild Ancestry of Cultivated Barley

The demonstration of the hybrid origin of *H. agriocrithon* casts grave doubts as to the validity of the hypothesis that cultivated barley originated from a six-rowed wild prototype. As already pointed out (Zohary 1959) this hypothesis becomes even harder to accept when one realized that *agriocrithon* forms are hardly adapted to disperse their fruit and to survive under wild conditions. Moreover, the very concept of a six-rowed wild progenitor, as advanced by Schiemann (1932, 1948), can be further challenged upon examination of the comparative morphology of the dispersal triplet in the genus *Hordeum*.

All known wild *Hordeum* species are distichous and have characteristic reduced lateral spikelets. The exception is the questionable *H. agriocrithon*. Although the genus *Hordeum* most likely evolved from an ancient prototype with fertile lateral spikelets, the fact that all existing wild species are distichous indicates that the distichous condition was attained already at an early stage of the differentiation of this genus—geologically long ago. Now that the seed dispersal biology of this group is understood, the reduction of the lateral spikelets should be regarded as an early trend of specialization in fruit dispersal. Accordingly, one would expect to find the relic six-rowed condition preserved in the less specialized perennial species. These are relatively less dependent on an efficient seed dispersal mechanism. Preservation of this relic six-rowed condition in a wild annual is most unlikely.

Another argument advanced by the advocates of the six-rowed ancestry of cultivated barley is the assumption that the evolutionary trend of reduced lateral spikelets is irreversible. If so, it is, of course, impossible to derive the six-rowed cultivated barley from a wild two-rowed type. (For details see Schiemann 1932, Takahashi 1955). In the present author's view, in the case of barley, the adherence to Dollo's "law" of irreversibility of reduced organs is erroneous. Genetic data

(for review see Hoffmann 1959) show that the difference between distichous and hexastichous conditions is controlled mainly by a single locus. The irreversibility argument can not be considered valid in cases where only one or few genes are concerned. Mutations from the dominant two-rowed condition (V) to the recessive six-rowed condition (v) cannot be expected to be encountered often in wild *H. spontaneum* populations owing to the strong selective pressure against them. Yet such mutations would most likely be detected if rigorously and properly looked for.

On the basis of the above mentioned considerations it seems highly unlikely that at the beginning of agriculture there ever existed a wild six-rowed form in the section *Cerealia*. It is much safer to assume that the distichous condition became established in the genus *Hordeum* already geologically long before the advent of agriculture and that wild hexastichous barley types existed only at a geologically early phase in the differentiation of this genus, prior to the establishment of the triplet as a trypanocarpous dispersal unit.

At the onset of agriculture, the section *Cerealia* of the genus *Hordeum* was most probably represented only by a single wild species, namely *H. spontaneum*, and this wild barley should be regarded as the progenitor for all cultivated barley forms. The reappearance of the six-rowed condition was made possible only after the breakdown of the wild mode of seed dispersal as a result of domestication.

Mode of Origin and Alterations under Domestication

The crucial step, and most likely the starting step, in the process of domestication of the brittle, two-rowed *H. spontaneum* was the selection by man for non-brittle mutants. In carrying out this selection man changed drastically the specialized mode of seed dispersal of the wild prototype and made harvesting feasible. The change from trypanocarpy to harvesting and threshing by man corresponds in fact to a "jump" into a new adaptive range (Simpson 1953). This done, the whole ensemble of characters associated with the wild mode of fruit dissemination became functionless and lost its adaptive value. It is the relaxation of this selective pressure that facilitated, to a large extent, the burst of a wide range of ear and spikelet variations encountered among cultivated barley lines. Mutations in many cases were no more disadvantageous and some were, intentionally or unintentionally, selected by man.

In the following section an attempt is made to point out the main morphological traits associated with the wild mode of seed dispersal and to sketch the trends of their alterations under domestication (For summary see also Table II). The evolutionary relationships between the main morphological types of barley, on the assumption of a two-rowed wild ancestry, are presented in Diagram 1.

a) *Alterations in the lateral spikelets:* These are perhaps the most conspicuous changes which became possible after the breakdown of the wild mode of seed dispersal. In *H. spontaneum* the stiff, awnless pedicellated lateral spikelets function as wings of the arrow-head of the dispersal apparatus. They effectively prevent any

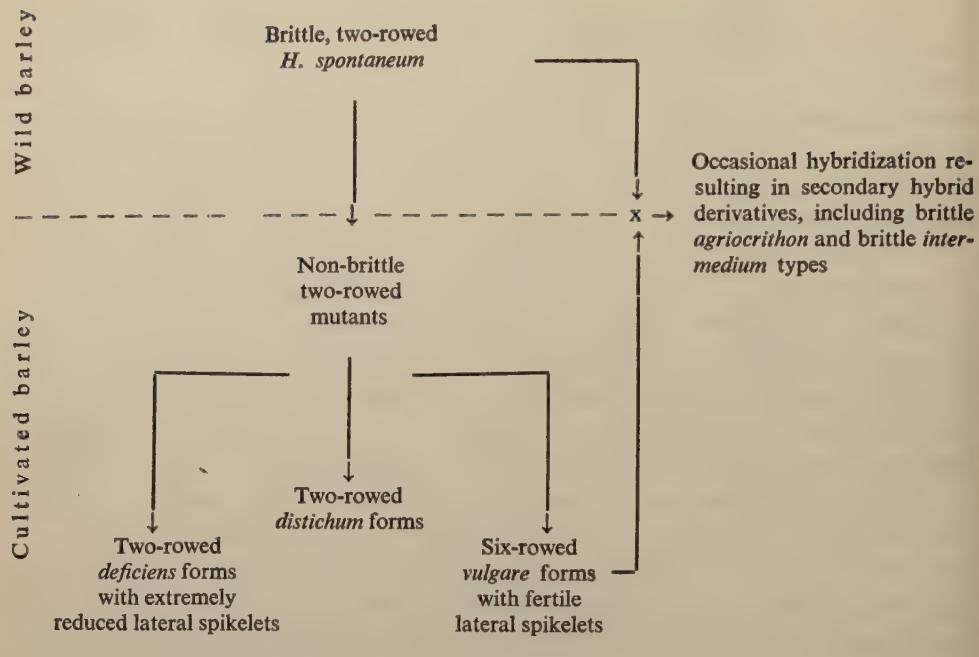


Diagram 1

Schematic representation of relationships between the main morphological types in the section *Cerealia* of the genus *Hordeum* on the assumption that *H. spontaneum* is the only true wild species in this section and the ancestor of all cultivated barley forms.

back-movement of the triplet after its insertion in the ground. Their size and structure are therefore rigidly maintained by natural selection.

While the primitive *spontaneum*-like condition is still almost unaltered in many cultivated *distichum* forms, two principal evolutionary trends opposed to each other are apparent under domestication. The first trend is a further reduction of the now functionless lateral spikelets culminating in their extreme reduction in the *deficiens* forms. A second trend is in the opposite direction: selection by man for complete fertility of the lateral spikelets and the establishment of the six-rowed *vulgare* forms.

b) *Compactness of the ears*: Another conspicuous evolutionary trend under cultivation is a gradual transition from lax to dense ears. As stressed by Schiemann (1948) the degree of compactness of the ear is determined by the length of the rachis internodes. In wild brittle barley this rachis segment functions as the point of the dispersal triplet. Its relative length is adapted to the wild mode of dispersal. Under harvesting, the establishment of denser ears became possible. A trend for denser ears

can be followed both in two-rowed *distichum* barley (*nutans* → *erectum* → *zeocritthon*) and in six-rowed *vulgare* barley (*pallidum* → *parallelum* → *pyramidalatum*).

c) *Hairiness of the rachis, rachilla and glumes*: The dense cover of upward directed long hairs which is characteristic of the edges of the rachis, the rachilla and the lower part of the glumes of *H. spontaneum*, is again apparently associated with the seed dispersal biology of this plant. The hairs facilitate the anchorage of the triplet and help to prevent back movement. In cultivated forms there is an obvious trend to reduce the density of hairs and also to modify their structure (e.g. change from "Landgerstentyp" *L* to "Chevalliertyp" *I*).

d) *Scabrosity of glumes, lemmas and awns*: The upward pointed dentation found on the upper part of the glumes and on the edges of the lemmas and the awns of *H. spontaneum* function again to resist backward movement of the triplet. Under domestication there is an apparent trend to reduce the scabrosity of these parts down to varieties with toothless lemmas and with smooth awns.

e) *Stiff long awns*: The long stiff awn of the middle spikelet in *H. spontaneum* functions to direct the fall of the triplet among the drying culms of the parent generation. Also by vibrating continuously in the wind it seems to help the anchored triplet in penetrating the ground. In addition, the stiff scabrous awns apparently serve to protect the ears from being grazed during the critical period of the flowering and the seed-set. It is a general observation of shepherds in Israel that inflorescences of *H. spontaneum* are seldom eaten by sheep and cattle, from the time of their emergence till after fruit dispersal. In cultivated barley one encounters a whole series of reductions of awn size down to awnless varieties as well as various modifications of its morphology with such extreme mutants as the hooded varieties.

TABLE II

Main morphological traits associated with seed dispersal in wild barley and the trends of their alteration under domestication

Wild characters	Alterations under domestication
1. Brittle rachis with sharp disarticulation points.	1. Non-brittle, tough rachis.
2. Stiff, awnless, scabrous pedicellated, lateral spikelets functioning as the wings of the arrowhead of the dispersal unit.	2. Two main trends of alterations: (a) further reduction of lateral spikelets; (b) restoration of fertility to lateral spikelets.
3. Relatively lax ears, with long rachis internodes.	3. Reduction in length of the rachis internodes, resulting in compact ears.
4. Hairy rachis, rachilla and glumes.	4. Reduction in the amount of hairs down to glabrous surfaces.
5. Scabrous glumes, lemmas and awns with upward pointed teeth.	5. Reduction in the amount of dentation down to lemmas and awns with smooth surfaces.
6. Stiff long awns.	6. Reduction in awn size down to awnless types; various modifications in shape and structure of awn.
7. Linear filiform, elastic glumes.	7. Alterations in the elasticity, size and shape of the glumes.

f) *Glume morphology*: The linear, elastic glumes characteristic of *H. spontaneum* are apparently also associated with the dispersal mechanism of the triplet. The lower part of the glumes is densely hairy, while their upper part is furnished with sparse upward directed teeth. Being elastic, the somewhat spreading glumes do not interfere with the downward penetration of the unit into the ground. They effectively serve as auxiliary attachments that resist back movement.

Under domestication one encounters a general trend to reduce the elasticity as well as the hairiness and scabrosity of the glumes. The general outline of the wild-type glumes is retained in most cultivated varieties. Drastic changes in this respect are found, however, in the *macrolepis* varieties.

The Breeding System and Its Significance

It is generally accepted by barley students that the breeding system of self-pollination serves as a main isolation barrier between barley forms and causes the splitting of this group into numerous lines. However, few if any workers have realized the full evolutionary implications of the fact that self-pollination here is incomplete and is accompanied by occasional cross-pollination. A small percentage of cross-pollination or "contaminations" between cultivated varieties have been repeatedly observed by barley breeders. The present study demonstrates that a similar gene-flow exists also between *H. spontaneum* and cultivated barley. It is therefore safe to assume that the *Cerealia* group is not composed of clusters of fully isolated entities. The various forms of this section have to be considered as genetically closely knit together.

Stebbins (1957) has already explored the evolutionary implications of a breeding system where the predominating self-fertilization is complemented by occasional cross-fertilization. He points out its similarity with Sewall Wright's model of population structure favourable for rapid evolution. In its breeding behaviour and in its range and pattern of variation, the *Cerealia* group can serve as an excellent example for Stebbins's theoretical model. For phylogenetic considerations such breeding behaviour implies that the evolution of the numerous barley varieties can no longer be regarded as linear and independent. Their origin is undoubtedly highly reticulate and most likely complicated even further by introgression from different local biotypes of *H. spontaneum* with which cultivated barley came in contact when agriculture spread. Any detailed constructions of linear phylogenies or a demonstration of independent parallel evolution within this group are therefore, to a large extent, meaningless.

For this reason no detailed phylogenies have been attempted in this work. Instead, an effort has been made to assess which characters are wild and which are derived under domestication. Only after such an analysis of characters has been made, can one proceed to evaluate which cultivated varieties are relatively more primitive (i.e. show a larger combination of wild type traits) and which are more advanced (i.e. show a larger proportion of derived traits).

Archeological Evidence

Recently Helbaek (1959) reported his find of two-rowed non-brittle barley in grain remains excavated at Jarmo, Iraqi Kurdistan. These archeological finds are estimated to date from the beginning of the 7th millennium B.C. and present us, according to Helbaek, with the earliest finds of the beginning of agriculture. The material is apparently admirably well preserved and includes critical specimens in which a lateral staminate spikelet is still attached to the median one. As pointed out by Helbaek it closely conforms with *H. spontaneum* in several morphological characteristics (e.g. pedicellate lateral spikelets).

Jarmo finds provide us with the critical archeological "missing link" for a demonstration that *H. spontaneum* should be regarded as the ancestor of cultivated barley. Helbaek should be credited with the first convincing archeological verification of the two-row hypothesis.

Place of Origin

If the two-row hypothesis is accepted, a revision becomes necessary also of the prevailing view on the place of origin of cultivated barley. If the sole ancestor of cultivated barley is indeed *H. spontaneum*, domestication should have occurred within the area of distribution of this species. One has therefore to reject the view of Schiemann (1948, 1951) and Freisleben (1940), namely that domestication originated in the East Asiatic gene centre of barley, and to return to the original suggestion of De Candolle (1884) that Western Asia is the place of origin of this cultivated plant. This is also borne out by the archeological evidence brought by Helbaek (1959).

The East Asiatic or Chinese variation centre of cultivated barley is apparently only a secondary or accumulation centre, similar in nature and development to the Ethiopian centre. To both areas barley was most likely introduced already as a cultivated crop. The almost complete lack of distichous barley forms in East Asia is to be attributed to early cultural preferences, as well as to the partial isolation of that region from Western Asia, which could have led to the early introduction of only hexastichous varieties there.

The difference between western and eastern varieties of cultivated barley in regard to the relative frequency of the two genes determining rachis stiffness, is to be considered in a similar manner. Takahashi (1955) demonstrated that the East Asiatic varieties are predominantly of the "E" type, namely, having a $BtBt\ bt_2bt_2$ genotype, while West Asiatic countries were found to include 60-80% of the "W" or $btbt\ Bt_2Bt_2$ genotype. However, the different geographical distribution of the two genes does not necessarily indicate a diphyletic mode of origin of cultivated barley, as proposed by Takahashi (1955). Both non-brittleness mutations could have occurred in *H. spontaneum* (which has a $BtBtBt_2Bt_2$ genotype) in Western Asia. Both could have been picked up independently by the early grain domesticators in that area. According to the diphyletic models the presence of the bt_2 gene in Western Asia is

explained by migration from Eastern Asia and by subsequent hybridization. But it is simpler to assume that its predominance in the Chinese centre of agriculture is the result of early chance introduction from the west (and most likely, in already six-rowed cultivated forms). Similarly, the fact that in Western Asia the "E" genotype is more frequent among six-rowed varieties than among two-rowed forms need not be explained by a western origin of the former, as required by the diphyletic hypothesis. Such a difference could have easily developed, if there had been relatively higher selective value to the bt_2 gene when in combination with the six-rowed condition.

ACKNOWLEDGEMENTS

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THE LEAF-FLORAL BUD RELATIONSHIP OF GENETIC SEXUAL TYPES IN THE CUCUMBER PLANT

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ABSTRACT

In the course of this study, the developmental relationship between age of leaves and floral buds in their axils was examined in different sexual types of *Cucumis sativus*. It was found that floral buds of the female forms (gynoecious and hermaphrodite plants) reach more advanced stages of development than buds developing near leaves of similar size on the corresponding male types (monoecious and andromonoecious plants). This is based on the fact that the differentiating floral bud reaches the critical turning point towards maleness or femaleness next to a younger leaf on a female plant, than does its equivalent on the male types.

It is suggested that such a morphogenetic difference is associated with a physiological difference, namely—the hormonal balance in the vicinity of the developing bud is more in favour of growth substances in the case of the female forms, while it is less so for the male types. This suggestion is deduced from the known role played by young and adult leaves in the balance of growth and inhibitory substances within the plant.

INTRODUCTION

It is well known that leaves play an important role in production of growth and inhibitory substances in the living plant. It is also assumed that young and adult leaves within one and the same plant are antagonistic in this respect, i.e. while the young leaves are active in producing growth substances, the adult ones destroy them and/or produce substances which counteract their effect. Hence, it might be suggested that one of the factors influencing the overall balance between these two classes of substances within the plant is the ratio of young to adult leaves.

Furthermore it has been shown recently (Laibach and Kribben 1950, Heslop-Harrison 1957, Galun 1959a, Wittwer and Bukovac 1958) that growth substances (or the balance between them and their antagonists) play a role in the sex expression of plants. Therefore it seemed worthwhile to find out whether genetic differences in sex expression are associated with a difference in leaf age pattern on the plant as a whole or in the immediate vicinity of the developing floral bud.

MATERIAL AND METHODS

Four genetic sexual types of the cucumber plant were used in this study: (1) *Monoeccious*—a pure line of the local variety Beit-Alfa. (2) *Gynoecious*—identical in all respects, except in sex expression, to type (1) and obtained by repeated backcrossing

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a female mutant to plants of a monoecious line of the variety Beit-Alfa (the latter used as the recurrent parent). (3) *Andromonoecious*—of the variety Richmond Green Apple, and (4) *Hermaphrodite*—obtained by introducing a gene for “femaleness” to type (3) (Galun 1958).

Degree of “femaleness” of the different types is described here according to Shifriss and Galun (1956), i.e. the number of nodes on the main branch to the first female flower (“node number”). Accordingly, type (1) has 8–9 nodes to the first female flower (at the season when the study was carried out); type (2) is female from the first node on, type (3) has 20 or more nodes to the first hermaphrodite flower (all lower ones were male), while type (4) developed hermaphrodite flowers from the first node.

The method for determining the developmental stages of the floral buds is described at length elsewhere (Atsmon and Galun 1960); stage No. 1 (Figure 2) is the hermaphrodite stage, through which all types of flowers pass; at this stage it is impossible to differentiate morphologically between the future male, female or hermaphrodite flower. Stages 2, 3, 4 and 5 denote successive steps in the further development of the buds: enlargement of male organs and relative diminution of their counterparts in the male buds; the reverse situation in the female buds and the further development of both male and female organs in the hermaphrodite bud.

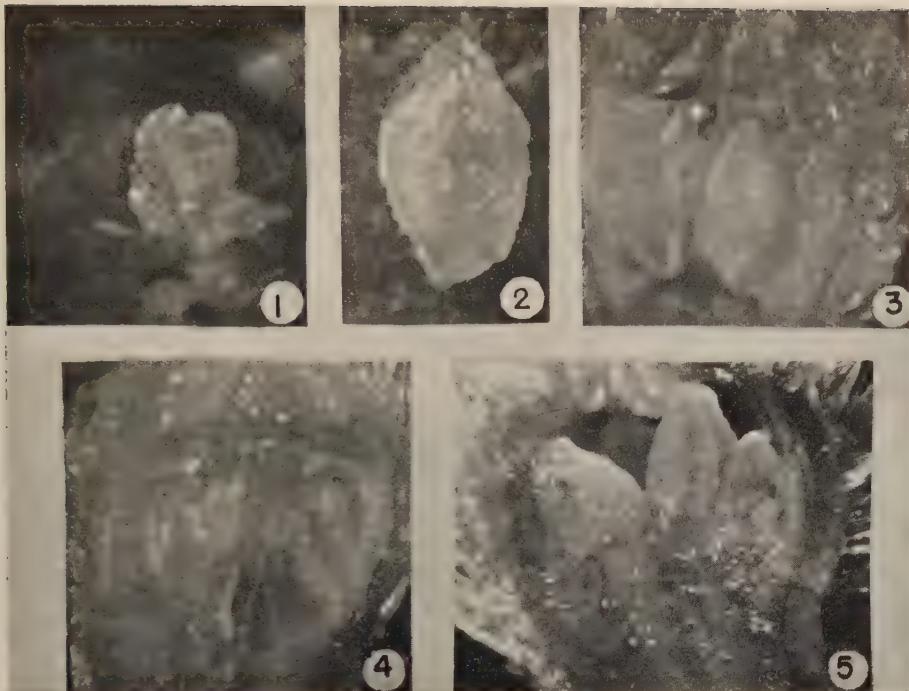
The developmental stage of the flower bud preceding stage No. 1, in which neither female nor male organs can be detected as yet, will be called “corona” (Figure 1). This stage was given the numerical value 0.7.

Eight whole plants of each sexual type were examined from base to apex, and floral buds were photographed. The plants were examined at different developmental stages, and three representative stages were chosen for node to node comparison. Only plants of similar vegetative development were compared.

RESULTS

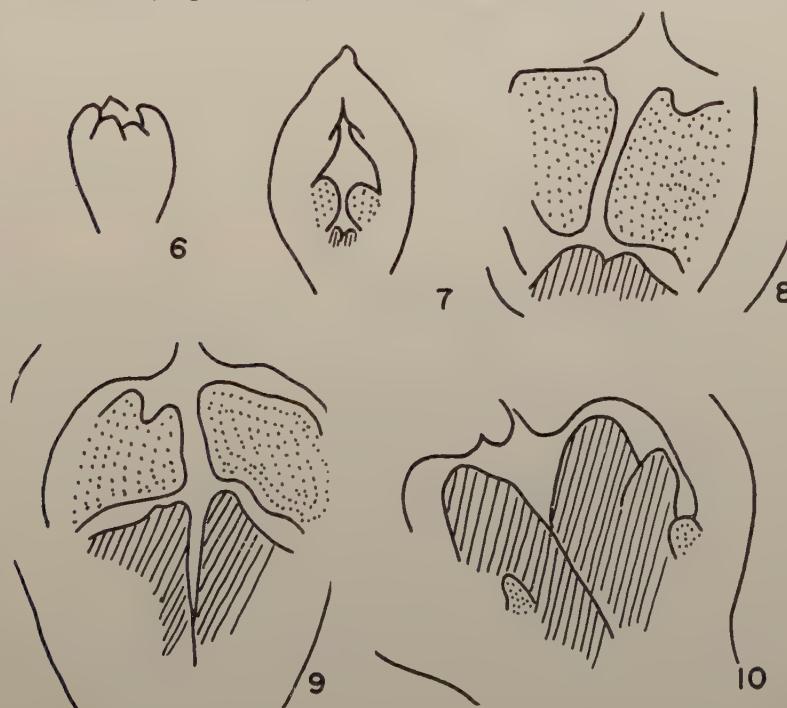
It was found (Table I) that floral buds develop earlier, in relation to leaf size, in the female types than in their corresponding male types, i.e. floral buds reach more advanced stages in the axils of young leaves in the gynoecious plant, as compared to male flower buds in the monoecious plant; the same is true for the hermaphrodite plant as compared to andromonoecious plant. In this last case the difference between the two types was usually greater than between the gynoecious and the monoecious plants, and this corresponds well to the greater difference in node number, i.e. in sex tendency, between the two types compared.

Figures 1, 3, 4 and 5 demonstrate a typical situation in this respect. The four buds photographed were all taken from the fourth node of four similarly developed plants belonging to the different sexual types. The difference in development is quite clear. While the bud from the andromonoecious plant was still in the “corona” stage, where no sex organs can be detected, the bud of the hermaphrodite plant was already at stage 3. The same relationship is true also for the two other types; the male bud in



Figures 1-5

Five developmental stages of cucumber flower buds. Figure 1—the "corona" stage; Figure 2—stage No. 1; Figure 3—stages No. 2-3 in a male flower bud; Figure 4—stage No. 3 in a hermaphrodite flower bud; Figure 5—stage No. 5 in a female flower bud. (All ca $\times 30$).



Figures 6-10

Interpretative diagrammatic drawings of Figures 1-5 respectively. Dotted areas—male organs; shaded areas—female organs. (All ca $\times 30$).

the monoecious plant was still at stage 2-3 while the female one in the gynoecious plant had already reached the advanced stage designated as number 5.

The situation as a whole may be visualized more clearly in the graphs of Figure 11, where the ratio of bud development stage to leaf length was plotted against the nodes.

It is quite clear that bud to leaf ratio in all stages of development of the plant is highest in the female types, especially in the later nodes. In other words, the higher the node the greater becomes the difference in bud development stage between male and female forms, and always in favour of the latter ones.

Another fact becomes quite evident from the data of Table I, though more information is still required. It can be seen that the gradient in leaf size as well as that in bud stage within the same plant is lower in the female types than in the corresponding male types, i.e. differences between leaves or buds in adjacent nodes are smaller in the female types. As a result, a floral bud situated in the axil of a young leaf of a female plant is topographically further removed from the nearest adult leaf, in comparison to a bud developing in the axil of a similar leaf on a male type.

DISCUSSION

As shown elsewhere (Atsmon and Galun 1960) all three types of cucumber flowers (male, female and hermaphrodite) pass ontogenetically through a common developmental stage, in which they are morphologically similar and in which the male and female organs are equally developed. Only later the three types diverge from each other, by the relative diminution of male or female organs (in female and male buds respectively) or further development of both in the hermaphrodite bud. Thus every flower bud is potentially hermaphrodite, and it might be assumed that its final nature is determined by inner and outer environmental conditions prevailing shortly before the visible sexual differentiation takes place.

On the basis of previous experimental work (Laibach and Kribben 1950, Galun 1959a) it is quite evident that the concentration of endo- as well as exogenous growth substances in the cucumber plant influences its sex expression. More specifically—concentration of growth substances is one of the factors which determine whether a specific flower bud will develop, beyond stage No. 1, into a male or into a female flower. For a more general discussion of this point the reader is referred to Laibach (1952). It should only be noted that there are at least two principal possibilities for the relationship between growth substances and the sex expression of the plant. The one is a direct influence of the hormonal balance on the differentiating bud, pushing it one way or another; the second possibility is an indirect effect of hormones through their general influence on the growth of the plant as a whole, and especially on that of the leaves. Which of the possibilities is the real one is still not clear. Yet it is evident that anything influencing the content of growth substances within the plant will also influence indirectly its sex expression. It is logical to assume that it is the content of

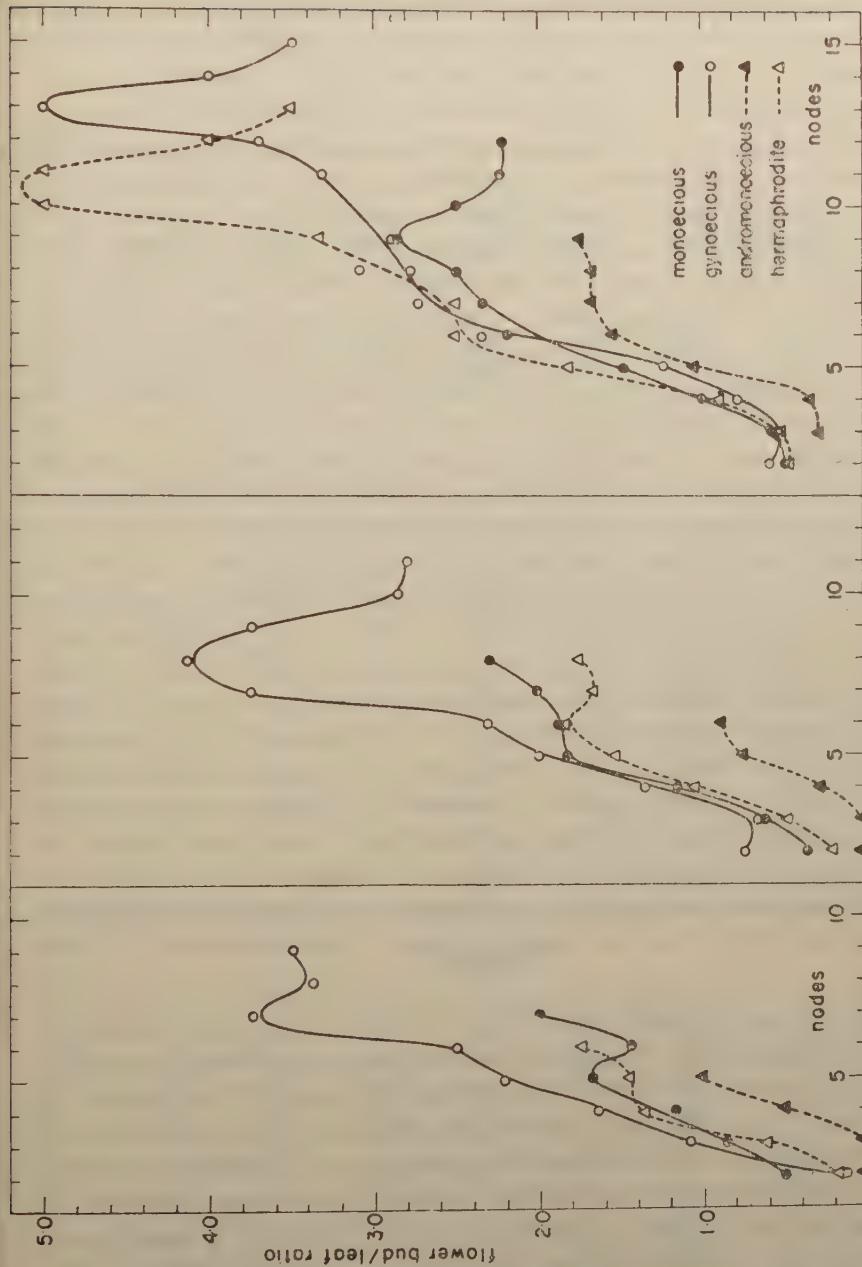


Figure 11

The ratio between developmental stage of flower buds (designated as stages 0.7 to 5) and length of leaves next to them (in cm) in the different nodes along the main branch. The three groups of curves illustrate the situation in three different developmental stages of the plants, earliest stage on the left, latest on the right. Data for these curves were taken from Table I.

TABLE I

Leaf length (in mm) and developmental stage of flower buds in three stages of plant development; four sexual types of the cucumber plant are represented. For further explanation see text.

Stage I									
	Monoecious		Gynoecious		Andromonoecious		Hermaphrodite		
Node No.	Bud stage	Leaf length	Bud stage	Leaf length	Bud stage	Leaf length	Bud stage	Leaf length	
2	3	60	1	72	0	67	1	65	
3	2-3	29	3-4	32	0	32	1	16	
4	2	17	2-3	14	*	14	1-2	11	
5	1-2	9	2	9	*	7	1	7	
6	1	7	1-2	6			*	4	
7	*	3.5	1-2	4					
8			1	3					
9			*	2					

Stage II									
	Monoecious		Gynoecious		Andromonoecious		Hermaphrodite		
Node No.	Bud stage	Leaf length	Bud stage	Leaf length	Bud stage	Leaf length	Bud stage	Leaf length	
2	2-3	70	5	65	0	78	1-2	75	
3	2-3	41	4-5	72	0	52	2	42	
4	2-3	22	5	37	*	26	3	29	
5	2	11	4	20	1	13	2	13	
6	1-2	8	3	13	*	8	1-2	8	
7	1	5	3	8			1	6	
8	*	3	2-3	6			*	4	
9			1-2	4					
10			1	3.5					
11			*	2.5					

Stage III									
	Monoecious		Gynoecious		Andromonoecious		Hermaphrodite		
Node No.	Bud stage	Leaf length	Bud stage	Leaf length	Bud stage	Leaf length	Bud stage	Leaf length	
2	5	105	+5	85	0	95	4-5	105	
3	5	90	5	95	2-3	87	5	100	
4	5	51	5	63	2	60	5	57	
5	4	27	4-5	37	2-3	24	4-5	25	
6	3-4	16	4	17	2	13	4	16	
7	3	13	3	11	1-2	9	3	12	
8	2-3	10	2-3	9	1	6	2-3	8	
9	2	7	2	7	*	4	2	6	
10	1-2	6	2	6			2	4	
11	1	4.5	1-2	4			1-2	3	
12	*	3.5	1-2	3			1	2.5	
13			1	2.5			*	2	
14			*	2					

* Bud at "corona" stage.

these substances in the immediate vicinity of the developing bud that is of importance in this respect, and therefore it is useful to study the inner and outer factors influencing it.

In order to make this suggestion clearer we might visualize the main branch of the developing cucumber plant as the site of four gradients: two morphological ones and two physiological ones. The two morphological gradients are: 1. Size of leaves, as an expression of their age, diminishing from the adult ones at the base to the primordia at the vegetative apex and 2. developmental stage of floral buds in the axis of the leaves, starting with fully developed flowers in the lower part of the branch and ending with "corona" and "cup"-like structures near the apex. The physiological gradients are: 1. the content of growth substances which is assumed to drop gradually from apex to base and 2. the content of anti-growth substances (in the broadest meaning of the expression). The direction of this gradient is opposite to the one above, i.e. highest in the region of adult leaves and lowest near the apex. Considering the role played by the age of the leaves in their influence on the hormonal balance within the plant, it seems quite legitimate to use the leaves as morphological landmarks for the assumed invisible two hormonal gradients. Thus any "shift" of the bud gradient in relation to the gradient of the leaves might be interpreted as a "shift" of any specific developmental stage in relation to the hormonal gradients. By "shift" of bud gradient we mean that the development of the floral buds is relatively retarded (or accelerated) and as a result one finds less (or more) developed buds in the axils of leaves which are similar in size. Such a "shift" means that the physiologically differentiating bud is surrounded by a tissue having a higher or lower content of hormones (growth substances or their antagonists). It is suggested that such "shifts" might constitute one of the factors accounting for differences in sex expression between plants, whether the primary cause for the "shift" is an environmental one, or a genetic one, as is the case studied here. It remains to be pointed out that the effect of such a "shift" is accentuated by the fact that it takes place along reversed gradients of antagonistic effects, i.e. descending along the one means *at the same time* ascending along the other.

As an example of such a "shift", resulting in a change of the sex expression, the influence of gibberellic acid (GA) in this respect may be mentioned. As already stated by Wittwer and Bukovac (1958) and Galun (1959b), GA pushes the sex expression of normal monoecious cucumber plants towards maleness. In the second work mentioned above (Galun 1.c.) it is also noted that GA retards flower bud development. It seems safe to suggest that the effect of GA on the sex expression works in this case through causing "bud shift" along the hormonal gradient, because buds reach the critical differentiation stage in the axil of relatively older leaves than in non-treated plants; this situation is brought about by the retarding effect that GA has on bud development while it does not have a similar effect on the leaves.

It is quite possible that environmental conditions like light and temperature, which

are long known to affect the sex expression of the cucumber plant, do this in a similar manner. Yet it should be pointed out that this leaf/bud relationship is considered only as one of several possible factors affecting the sex expression of the cucumber plant.

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